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LIFE AND EVOLUTION

AN INTRODUCTION TO GENERAL BIOLOGY

BY

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PREFACE

The aim of the present volume is to serve as an introduction to the study of biology. The subject-matter has been chosen to meet the needs of general students rather than prospective specialists in different branches of the science. Biology has exerted a profound influence upon psychology, sociology, ethics, philosophy, and many other fields of human knowledge, and, in these days, no one who is entitled to lay claim to a liberal education, can afford to remain ignorant of the rudiments of this subject. In so wide a field there is an almost unlimited opportunity for the choice of material to present, and doubtless several topics have been omitted which, in the opinion of many readers, should have been discussed. It has been my aim to present those aspects of biology which would best prepare the student for appreciating the great changes in our outlook upon the world which have resulted from discoveries and generalizations in regard to living forms. Considerable space has therefore been devoted to the doctrine of organic evolution, and the related topics of heredity, variation, and eugenics.

Although this book is intended for use as a text in colleges and universities, I have avoided the common pedagogical devices of subdividing and labeling the contents, and have endeavored to make the volume one that can be read in a normal manner. It is hoped that the book may prove useful also to the general reader who may be curious in regard to the content and import of modern biology.

I am indebted to my colleagues, Dr. C. A. Kofoid, Dr. Karl Meyer, Dr. J. Grinnell, Dr. C. V. Taylor, Dr. L. J. Strong, Dr. C. L. Camp, Mr. S. F. Light, and Mr. H. C. Hinshaw of the University of California, for critically reading several of the chapters. The entire manuscript has been read by Dr. H. B. Torrey who has made several useful criticisms and suggestions.

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LIFE AND EVOLUTION

CHAPTER I

THE LIVING AND THE NON-LIVING

Biology is the science of life. In its broadest sense it includes all the knowledge that has been amassed concerning living things. Botany, which deals with plants, and zoölogy, which treats of animals, are therefore subdivisions of the broader field of biology. Through one of those curious coincidences that sometimes occur in the history of science, the word "biology" was coined independently and in the same year, 1802, by two naturalists, Lamarck and Treviranus, in order to have an appropriate designation for the general science of living organisms. Sometimes the term "biology" has been used to signify knowledge of the habits and adaptations of organisms, but in the present volume it will be employed in its wider and more usual meaning.

It is much easier to define the science of life than it is to define life itself, and there is probably not much use in attempting a definition of life at the present stage of our progress. Most of us know pretty well what we mean by this term, even if we find difficulty in properly expressing our meaning in words. In his *Leçons sur les phénomènes de la vie,* which is one of the classics of biological literature, the great French physiologist, Claude Bernard, contends that our efforts to define life are quite as futile, and add as little to our knowledge, as our endeavors to define space, time, matter, and many other common phenomena of our daily experience. We may find it of interest to consider some definitions of life later on, but for most practical purposes we can get along, without the least confusion, with the common-sense notion of the subject which every one has. No one is

likely to confuse a dead cat with a living one, at least for long. We may be deceived for a time by an insect that is feigning death, but our doubts are immediately dispelled when the creature begins to use its legs. We may not be able to tell at first whether a seed is alive or dead, but if it develops into a plant, we no longer doubt. It is still more rarely that we confuse animate creatures with the so-called inorganic bodies which have never enjoyed the experience of living. There is a story of a Scotch soldier who picked up a watch and concluded from its movements that it must be alive. With the characteristic thrift of his people, he disposed of it soon afterward and remarked that "he was right glad to get rid of the creature, for she died no long time after he caught her." But even if the soldier had never seen or even heard of a watch before, he must have been a very stupid sort of person not to have recognized it as a mechanism of human contrivance.

The distinction between the living and the non-living is one of the most fundamental and easily recognizable that is presented by the world in which we live. There is, however, a good deal of debate among scientists and philosophers as to just how fundamental this distinction really is. Many classes of things in this world, although separable without the least difficulty in ninety-nine cases out of a hundred, nevertheless grade into each other, or present differences here and there from the usual condition, so as greatly to perplex us when we try to define them with absolute precision. We are not apt to mistake an animal for a plant when we are dealing with their higher representatives, but when we study the simplest plants and animals, the distinction, as we shall find later on, is by no means always easy to make. And although we are rarely mistaken in telling the living from the non-living, we find it much more difficult to set up any *absolute* criteria by which they may be distinguished. This truth will become more apparent, I think, when we pass in review some of the outstanding differences between living and dead things. The great English biologist, Professor Huxley, specified as the distinctive properties of living matter: (1) its

chemical composition; (2) its universal disintegration and waste by oxidation and its concomitant redintegration by the intussusception of new matter; and (3) "its tendency to undergo cyclical changes." These characteristics serve fairly well to delimit living substances from lifeless material. There are also several other properties that serve the same purpose. I have therefore compiled a somewhat more extensive list of differentia than Professor Huxley did, although most of the following may really be implied in, or deducible from, those which I have just quoted from this authority.

As regards their chemical composition, living organisms are distinguished by the extraordinary complexity of their component molecules. All living matter contains the elements oxygen, hydrogen, carbon, nitrogen, sulphur, and phosphorus. Commonly also it contains potassium, sodium, calcium, magnesium, iron, chlorine, and iodine. More rarely do we find in it the elements copper, manganese, fluorine, and silicon. Every organism includes a certain amount of material which is not really alive, namely, water, inorganic salts, food materials, waste products, and sometimes supporting substances, such as the limy material of our bones, and the cellulose framework of plants. These are the mere adjuncts or accidents of the process of living. The substance that is supposed to be the vehicle of vital activity is a jellylike material called protoplasm, which is sometimes spoken of, in Huxley's famous phrase, as the physical basis of life. Protoplasm is now recognized to be not merely one substance, but a collection of substances of a high degree of chemical complexity. It has thus far resisted accurate chemical analysis, and nothing closely approaching it has ever been fabricated by the skill of the chemist. So far as is known, it is produced only through the agency of life.

One of the most distinctive of the characteristics of living things consists in the kind of change which their living protoplasm undergoes. Protoplasm is subject to a twofold process of waste and repair, which is called metabolism. On the one hand, the food materials are built up into more and more complex sub-

stances (anabolism), and these are again broken down (katabolism) into simpler and simpler constituents, which are finally eliminated. When building up predominates over breaking down, there is growth. The growth of living matter takes place not by the addition of materials to the outside merely, as in the growth of most non-living things, but throughout the mass by a process called intussusception. In this growth there is an assimilation by which nutrient material is made over into the kinds of protoplasm characteristic of the organism. Whether we dine on beefsteak, chicken, oysters, or plain bread and cheese, the molecules of these foods are first broken down into a readily absorbable form, and are then taken into the cells of our body and converted into our own peculiar varieties of living tissue. If these same foods should fall to the lot of a dog or a pig, they would be transformed into the somewhat different protoplasms peculiar to these animals. Each kind of protoplasm has the remarkable property of building itself up out of a great variety of different materials. There are as many kinds of protoplasm as there are kinds of organisms, and there are probably millions of different kinds of organisms. This physical basis of life is the scene of continuous transformations in which construction and destruction are always involved. During metabolism many compounds are broken down and oxidized, and then eliminated. By this process of oxidation, and by other processes also, there is yielded a supply of energy which is employed by the organism in carrying on its functions. Oxidation plays a rôle in metabolism similar to that which it performs in burning the coal in the furnace of an engine. It furnishes the energy for running the machine.

The process of metabolism is found in all things that live. It may be said to be the central and basic feature of the life process. Because it furnishes the material and the energy for the business of living, an understanding of the various steps involved in its course would bring us very close to discovering the fundamental secrets of life itself.

There seems to be nothing quite like metabolism in the in-

organic world. A crystal may grow if placed in a solution of its own substance, and if other substances are also present in the solution the crystal picks out and adds its own kind of material. There is a resemblance here to growth by assimilation. Of late years several investigations have been carried on with so-called liquid crystals. These are said to grow, not as a solid crystal grows by external accretion, but by incorporating the new material throughout their mass, *i. e.*, by intussusception. But the liquid crystal does not build up its substance out of materials of a different nature; it simply uses its own kind of molecules, that are already available.

There is a closer analogy with the growth of a candle flame. The flame, like a living organism, is the scene of constant chemical transformation. Wax or tallow is drawn into it, volatilized, and burned. Oxidation supplies the energy for the process of combustion, and it plays much the same rôle in the life of an organism. Matter is drawn through the flame, as it is through a living being, and the flame under favorable conditions may grow, the materials composing it being added throughout its mass. If we may speak of the substance of the flame (for like protoplasm it really contains many kinds of substances), the flame may be said to grow by converting its food into its own characteristic material. Here we have something that is at least analogous to metabolism and growth by assimilation. From the chemical standpoint, however, the processes are, for the most part, purely destructive.

Another general feature of living things is their tendency to assume a fairly definite size, which is characteristic of a given kind of organism, although exceedingly variable in different kinds of organisms. This means that each kind of living creature, when it reaches about a certain size, stops growing. Naturalists in describing a species commonly specify its average dimensions, or the limits of size between which it is apt to vary. At the one extreme we have those organisms, the filterable viruses, which pass through all ordinary filters, and are too small to be visible through the most powerful microscope; and at the other, the

gigantic whales, and the mammoth redwood trees of California. This relative constancy of adult size is a very general characteristic of living things, although it is by no means one of their exclusive properties. Many other things, such as atoms and molecules, may be very uniform in size, although in the inorganic world this uniformity may usually be due to other causes than the cessation of growth. No one, so far as I am aware, has ever explained why the atoms of any given element are practically alike, and of nearly, if not quite, the same size.

Along with relative constancy of size, living beings typically exhibit a relative constancy of form. The material of which they are composed undergoes a continual change, without entailing much change of form or structure. Living beings have often been compared to vortices, whose form remains the same, but whose substance is never twice the same. The form of an organism may be retained despite agencies which mutilate or distort it. A salamander may regenerate a leg or a tail, and a Hydra may form a new body from a short piece of its stem. This power of restoration, although varying greatly in extent, is exhibited to a greater or less degree by all living things. Without it, life in any organism would not be possible. Were I to maintain, however, that this fortunate property is an exclusive possession of living organisms, I should probably be reminded that broken crystals are also able to regenerate if they are placed in a solution of their own substance. Some have thought that the regeneration of a crystal and the regeneration of a salamander's tail are fundamentally akin. This, at least, is a debatable point, and illustrates the difficulty of being sure about *absolute* distinctions between the living and the non-living.

Living beings, however, have a way of changing their form in successive periods of their life—they undergo cyclical changes. The living organism is not a static thing like a crystal; it represents a dynamic equilibrium. What it tends to regenerate, therefore, depends upon the period of its life cycle in which the regenerative activities occur. With higher organisms the cyclical changes involve growth, development, and finally natural death

and dissolution. Life leads to death as the final term of its own natural course. The life history may be run through quickly. It may have, as with man, a normal period of threescore and ten years; it may be prolonged through many centuries, as in the giant redwood trees of California, some of which were already old when Plato taught in the Academy. Whatever the allotted term of their existence, all higher organisms at least are like clocks, designed to keep going for a given length of time, but inevitably destined to run down and stop.

Correlated with the tendency of life to pass through a cycle of changes, is the power of organisms to give rise to other organisms of the same kind, *i. e.*, the power of reproduction, which insures the perpetuation of life, despite the inevitable death of the individual organism. Some of the simplest living things may not be subject to natural death, since they simply divide into two parts, each of which goes on living; but these organisms pass through a series of changes from one division to the next, slight as these may be in the most primitive types. All organisms reproduce and undergo a process of development. This is one of the most distinctive features of living things, but it may not set them apart absolutely from inorganic objects. Several crystals may arise from the broken fragments of a single crystal, but this kind of reproduction differs from that occurring in an organism by being imposed from without, instead of occurring as a result of the inherent activity of the object. Certainly objects as a rule do not grow, develop, and divide, unless they are alive.

Another universal feature of organisms is irritability, or the property of responding to stimuli. If we happen to touch a hot stove, we respond to the stimulus of heat by jerking back, and perhaps also in other ways. Even plants may respond to stimuli by turning their leaves and stems toward the sun, and by sending their roots toward moisture in the soil. Much of life consists of responding to stimuli in one way or another. The ability to react makes possible the science of psychology, which is concerned with the ways in which organisms, especially animals, behave.

If I should say that only organisms are irritable, I fear that an opponent might present me with many instances in which inanimate objects react to forces that impinge upon them. Should I handle a stick of dynamite with inconsiderate roughness, the response might be more violent than I should desire. A piano responds when I press the keys, and a piece of ice melts in response to the application of heat. Perhaps there is nothing in these reactions of inanimate objects that is essentially different from response in the living organism. A Hindu physiologist, J. C. Bose, has written an interesting book entitled *Response in the Living and Non-Living*, in which he shows that even metals respond to stimuli by showing fatigue and recovery, and by exhibiting other features of behavior that closely parallel the reactions of living matter.

I come finally to a peculiarity which has often been held up as the very essence of life—the power of adaptation. In an organism, as a rule, activity is directed into useful channels, and the organs by which activities are carried on seem to be especially fitted for their work. Our hands are wonderfully adapted for grasping and manipulating objects, our ears for hearing sounds, our lungs for carrying on the function of respiration, and our hearts for propelling blood. In the plant the leaves, stems, roots, flowers, and fruit are similarly fitted for carrying on their respective functions. Everywhere in the organic world we meet with an adjustment of organ to function. Everywhere nature teems with adaptive contrivances which secure the welfare of her living creatures. The hinge on the bivalve's shell, the protective spines of the sea-urchin, the downy pappus that enables the seeds of the dandelion to be scattered by the wind, the hooks by which the tapeworm keeps its hold on the intestinal wall of its host, are a few among the millions of adaptive devices which the organic world presents.

And it is not only in structural mechanisms that adaptations are shown; they occur even more plentifully in physiological activities and in behavior. The presence of food in the stomach is responded to by setting into action the processes of digestion;

injurious stimuli evoke movements of avoidance; the sight of prey arouses the activities of pursuit in the hungry lion. These actions are adaptive in the sense that they assist in maintaining the life of the organism. Other acts may be serviceable in perpetuating the life of the race. For this end there are specialized mechanisms for reproduction, and instincts for the care of offspring. The mammary glands are adapted by structure and function to supply nutriment to the young, and the latter are adapted to take advantage of this source of food by sucking, swallowing, and digesting. It is obvious that without this highly adaptive instinctive propensity to suck, the whole class of mammals, including ourselves, would speedily become extinct. All living things manifest adaptiveness. These adaptations are not in relation to an external end, like that of a watch for keeping time, for it makes no difference to the watch whether it keeps time badly or well. The end which is served by the organic adaptation is the welfare of the organism concerned. As the wise naturalist-philosopher Aristotle observed over two thousand years ago, life has its end in itself.

Vital activities center about two things, the preservation of the individual organism, and the perpetuation of its race. If we study the various things which organisms do in the course of their life cycle, we shall find that these two employments are what they are engaged in most of the time. In other words, life is bent upon its own continuation. The plant, in absorbing water and nutrient materials from the soil, in developing new buds and shoots, in turning its leaves so as to catch and utilize the rays of the sun, in exhibiting the beautiful color of its petals, and exhaling the fragrance of its nectaries, is simply acting, in one way or another, so as to preserve and enhance its own life, and to provide, through maturing fertile seed, for producing other plants like itself. The life of the lion in seeking prey, avoiding danger, mating, bearing offspring, suckling and protecting them, and later bringing food to the lair to satisfy their lusty growing appetites—the whole round of its varied activities— is dominated by the same fundamental endeavor to preserve and perpetuate

its kind. So it is with life everywhere. All organisms are engaged in playing essentially the same game, the game that is as old as life, and that will be played as long as life continues on the earth. It is the game of getting on—succeeding in self-perpetuation and in making provision for the offspring.

If we recur now to the definitions of life to which we previously alluded, and examine some of them which have been proposed, we shall find that they commonly refer to this adaptiveness of life as its chief distinguishing characteristic. Schelling defined life as "individuation"—not a very lucid definition at the first encounter, but a little reflection upon it shows that it emphasizes those self- and race-perpetuating features in which organic adaptiveness consists. G. H. Lewes defined life as "a series of definite and successive changes, both of structure and composition, which take place within an individual without destroying its identity," thus emphasizing, as did Schelling, the element of self-preservation. Herbert Spencer defined life as "the continuous adjustment of internal relations to external relations." Organisms are continually changing within to meet or adjust themselves to changes occurring without. But what is adjustment? Is it not a change which enables the organism to maintain itself, or in other words an adaptive change? Life then is a process of continuous adaptation. Or again, take the definition of Bichat: "Life is the totality of functions that resist death." While this statement has been criticized because it defines life in relation to death, a term which is intelligible only when contrasted with life, the definition really makes self-preservation and race-perpetuation the essential marks of vital activity.

Is this tendency to maintain individuality by a series of adaptive changes a unique possession of living beings? Many objects resist destruction because they are hard or tough. A crystal goes further and ekes out its mutilated form by adding material to its broken surface. A candle flame will quickly regain its regular form after distortion. These are, in a sense, self-preservative reactions, however different they may be from those exhibited by a living organism. Perhaps it is possible to

specify ways in which the adaptive reactions of living beings differ from those of inanimate objects, but even if no absolute distinction can be made, the various peculiarities of life which we have considered constitute a group of characteristics which probably does not occur in its entirety in anything but a living organism. Perhaps we should not be too sure of the truth of this statement, however, for we must bear in mind that life, although apparently a very distinct type of behavior, is carried on in the most intimate relationship to the inorganic world upon which it depends. Possibly all the component processes which are involved in living may occur also in non-living material. Life then would result from their combination in a harmonious and permanent relation.

That living beings derive their material directly or indirectly from the inanimate world goes without saying. It is also true that the energy for carrying on vital processes comes from outside sources, and for the most part directly or indirectly from the radiant energy of the sun. One of the most important scientific discoveries of the nineteenth century was the law of the conservation of energy, which was established through the labors of Mayer, Joule, Helmholtz, and Grove. According to this law, the energy of any closed system is constant in quantity, although the various forms of energy may be transformed into each other, as when friction produces heat, which in turn may give rise to light, sound, electrical energy, or mechanical work. Organisms, so far as careful experiment and measurement can determine, perform their functions in strict accordance with this fundamental principle. They are vortices in relation to the energy which passes through them quite as much as they are with respect to their component materials. The energy which I expend in writing these words is yielded chiefly by the combustion of carbohydrates in my muscles. These carbohydrates are the product of the constructive metabolism of plant life, the energy of the sun being utilized to build up these compounds out of the simpler constituents absorbed from the soil and air. I simply transform and direct the stream of energy that flows

through my body, without being able either to add to or to subtract from the total amount.

There are many different opinions as to how life is related to the processes of inanimate nature. As science has advanced, more and more of the phenomena of nature have been found to take place in accordance with uniform laws. The changes going on in inanimate things are commonly conceded to occur in conformity with the laws of physics and chemistry. Even the weather, fitful and unpredictable as it may be, we consider as controlled by uniform physical and chemical processes, a complete knowledge of which would enable us to forecast changes with a high degree of accuracy. While weather forecasting is a notoriously unsafe kind of prophecy, the scientist attributes this circumstance to the inadequacy of his knowledge of all the elements involved in his problem, and not to any failure of nature to conform to perfectly definite and invariable rules of procedure.

But how about life? Can it be similarly explained in physical and chemical terms? This is the question at issue between the mechanists who hold that life can be so explained, at least theoretically, and the vitalists who contend that it cannot. There are many brands of vitalism, but according to most of them, life activities are somehow controlled and directed by purpose. Life is a kind of purposive striving, bent on accomplishing its own perpetuation. It is fundamentally a teleological, or end-seeking process. Mere physics and chemistry, according to the vitalists, are not adequate to account for the purposive character of living. Physical and chemical changes, they admit, take place in living matter, but these changes are subject to a directive agency, which makes them carry out its conscious or unconscious purpose, much as the powerful engines that propel an ocean liner are guided by the will of the captain. All of the machinery in the engine room may work in strict accordance with the laws of physics, but whether the vessel goes into port at Hongkong or Manila depends upon the guiding purpose of the man at the helm.

The controversy between mechanism and vitalism has been

carried on from the time of Aristotle, who was a thoroughgoing teleologist, to the present, when both sides of the question are represented by able and scholarly defenders. The question at issue is one of fundamental importance, and one to be kept in mind by the reader as he goes through the rest of this volume. When he gets to the end he will possibly be somewhat better prepared to form an opinion on this mooted question.

The fundamental aim of the biologist is to understand the processes of life. Most vitalists, I think, would admit that knowledge of the physical and chemical changes that occur in living tissues would be of the highest importance. Certainly vital activity is conditioned by, if it be not completely explainable in terms of, the physical and chemical properties of the substances constituting protoplasm. I think it must be conceded that a part, at least, of the processes of living are already susceptible of explanation in chemical terms. There may always remain a residue which may serve as a subject for controversy. But if the position of either the mechanist or the vitalist is ever proven to be correct, it can be done so only by an intimate knowledge of fundamental life processes. Whatever standpoint is adopted, we should attempt to explain in mechanistic terms as much of vital activity as possible. For the vitalist, this would serve the purpose of revealing more clearly the elements involved in life, if there really are such, which are not capable of a mechanistic explanation. If all of the life processes are explained in terms of chemical and physical laws, the mechanist has won his case.

We shall not attempt to pursue the varied and subtle modifications of vitalistic theory. Historically the doctrine is a lineal descendant of the animism of primitive man. In the light of advancing knowledge, the cruder forms of vitalism have largely disappeared and have given place to more refined forms less obviously opposed to the results of scientific discovery Many physiologists have felt compelled to appeal to something different from the ordinary forces of nature in order to account for the constructive and coördinating processes of life. It has been asserted that natural forces, left to their own guidance, are ca-

pable only of destruction. When life leaves the body, things fall into ruin and decay. Life apparently has to struggle against these forces of nature. Claude Bernard, one of the greatest of physiologists, declared that "vital phenomena have their physico-chemical conditions rigorously determined," but at the same time the organism "appears to be directed by some invisible guide in the course which it follows. . . . The vital force directs the phenomena, which it does not create; physico-chemical agents produce phenomena which they do not direct." Bernard, like later vitalists, is desirous of adopting an interpretation of control which does not get him into trouble with the doctrine of the conservation of energy. But can energy be directed and controlled by anything which is not a source of energy in itself? On this question there is no end of subtle discussion. The captain, in controlling the course of his ship, may use relatively little energy, but he must use some. Whether there is a place for real teleological control in a world run, as ours seems to be, in accordance with the rigid laws of matter and motion, will probably be discussed for a long time to come.

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CHAPTER II

PROTOPLASM, OR THE PHYSICAL BASIS OF LIFE

The idea that life is everywhere associated with and dependent upon a peculiar substance called protoplasm has become a commonplace in biological thought. It gained wide currency as a result of a famous discourse delivered in 1868 by Professor Huxley, in which he referred to protoplasm as "the physical basis of life." As Professor E. B. Wilson has remarked, in another excellent, though much more recent address on the same topic: "Huxley's presentation of the subject was a masterpiece both of English style and philosophical breadth of outlook. In part for this reason, still more because of its supposedly materialistic implications, it aroused immediate and widespread public attention." But although Huxley disclaimed any belief in materialism, holding it "to involve a gross philosophic error," he failed to forestall a flood of criticism that was directed against him from pulpit and press. The notion that life in man, worm, plant, and protozoön, is in essence the same, and dependent on much the same kind of chemical substances, came as a shock to many of Huxley's contemporaries. But, as is the case with so many other disturbing ideas, now that it has become familiar it is found to be quite innocuous.

In some respects the concept of protoplasm, as presented by Huxley, has been found to require modification. Protoplasm is not a single complex compound, as many of Huxley's statements implied. It is doubtless an aggregation of many complex proteins, together with various other substances, which are equally essential to the maintenance of life. Protoplasm, as Hertwig states, is a "biological concept." And it is not the same chemically in different organisms. Chemical analysis clearly indicates that the component substances found in the protoplasms of the

different forms of life are different both in regard to their more highly organized and unstable protein molecules, and also in regard to their simpler constituents, even down to their prevalent mineral salts. But notwithstanding all these differences, there are many properties of protoplasm which are common to practically all forms of life.

When we look at this physical basis of life under the microscope, we perceive a semi-transparent, jellylike substance, usually part way between the fluid and the solid state. Some-

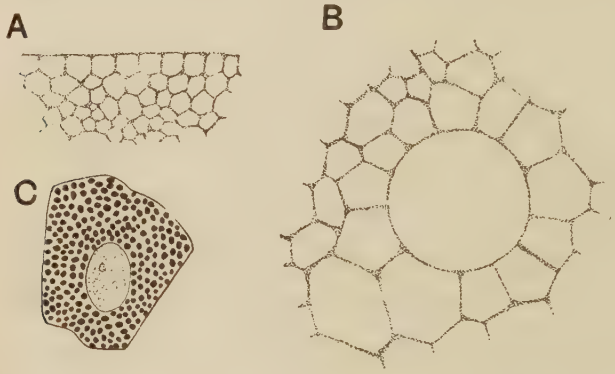

FIG. 1—*A*, an emulsion of olive oil and water showing a typical foam structure; *B*, the protoplasm of a radiolarian showing foam structure (from Bütschli); *C*, a liver cell showing granules. (After Altmann.)

times protoplasm appears, even under the highest powers of the microscope, to be entirely homogeneous. Again, it may have the appearance of a fibrous network; but the most typical structure is that of a sort of foam work, in the cavities, or alveoli, of which there is commonly material of more fluid consistency. The network appearance of protoplasm under a microscope is explained by Bütschli as the result of a foam structure, the walls of the alveoli appearing like interlacing fibers. By making an emulsion of olive oil in a solution of potassium carbonate, Bütschli has produced a fluid which appears under the microscope much like ordinary protoplasm. If very fine particles are added to the fluid, they come to lie in the nodes of the apparent network where

granules are generally found in living substance. The granules are of very frequent occurrence in protoplasm, and Altmann has advanced the theory that living substance is composed of discrete, but very minute granular elements which he calls bioblasts. Undoubtedly many of the granules observed in protoplasm are formed of living material, although many others represent mere products of protoplasmic activity.

Probably no one of the theories regarding the structure of

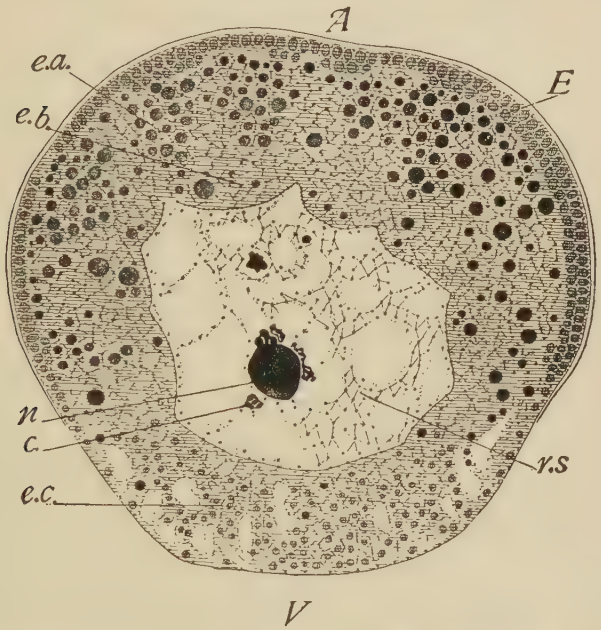

FIG. 2—A section across the egg of the worm Chætopterus showing the network structure of nucleus and cytoplasm: *A*, animal pole; *V*, vegetal pole of egg; *E*, granules of the ectoplasm, or outer layer; *e.a.*, *e.b.*, *e.c.*, different kinds of granules in the endoplasm; *c*, chromatin of the nucleus; *n*, nucleolus; *r.s.*, nuclear network. (After Lillie.)

protoplasm is universally and exclusively true. Living matter may assume many forms, becoming in different tissues fibrillar, alveolar, granular, or quite homogeneous in composition. Even the same protoplasm may assume different forms at different times. Protoplasm differs greatly in appearance according to

the kind and amount of other materials which it includes. The alveoli may contain a watery fluid, fat globules, yolk spheres, and various solid products of metabolism, such as starch grains, glycogen, pigment granules, and crystals. Some of these are substances which may be utilized as food, while others represent products of the breaking-down processes of living matter. There are many kinds of substances found in protoplasm, but those which are of the greatest importance are the following:

The Proteins. These are complex compounds containing carbon, oxygen, hydrogen, nitrogen, and frequently also phosphorus, sulphur, iron, calcium, sodium, potassium, magnesium, and more rarely other elements. Examples of proteins are furnished by albumen, which occurs in the white of egg; the casein of cheese; and the protein of muscle fiber. Many of the proteins are soluble in water, from which they may be precipitated by the proper reagents. Most of them can be coagulated by heat and various chemicals. Their molecules are relatively large and complex, and they may be broken down by enzyme action into simpler and simpler compounds. The simpler compounds which are formed by this process afford many clues as to the way in which the protein molecule is constituted. Among the simplest products of protein decomposition are the amino acids, of which there are many kinds. Starting with the amino acids, chemists have succeeded in synthesizing compounds having many of the properties of the simpler proteins. On account of the number of different groups of substances composing protein, there is the possibility, through making different permutations and combinations of these components, of producing an almost infinite variety of protein molecules. In the hemoglobins alone, as Reichert and Brown have shown, there is a special type of compound characteristic of the different species of vertebrate animals. Hemoglobin is an iron-containing protein which forms the chief oxygen carrier of our blood, and which gives to the blood its red color. It forms crystals whose shape depends upon the kind of animal from which it is derived, and it is probable that these peculiarities in crystalline form are indicative of differences in chemical

composition. In fact, there are many other indications that such chemical differences occur. There seems to be an almost endless variety of possible hemoglobins. And there is evidence that many other classes of proteins include an equally extensive series.

The carbohydrates are composed of carbon, hydrogen, and oxygen, the two latter elements being in the proportion in which they occur in water, H_2O. They have the general formula $C_x(H_2O)_y$. Common examples of carbohydrates are starch, sugar, and cellulose. Carbohydrates are less complex and more limited in number than the proteins, but, like the proteins, they may be split up by enzyme action into simpler compounds.

The fats, like the carbohydrates, contain the three elements, oxygen, carbon, and hydrogen, but these elements have a quite different arrangement, and hence cause the fats to differ markedly from the carbohydrates in their properties. Chemically fats are compounds of glycerin, $C_3H_5(OH)_3$, with some fatty acid. We are all familiar with fats as they occur in butter, meat, and the oils of plants. Fats, like carbohydrates, are important food materials and are utilized especially for the production of energy.

The Vitamines. In addition to the classes of foods just mentioned, there are other substances known as vitamines which have been found essential for the life and growth of many kinds of organisms. Until a few years ago, the existence of these important substances was entirely unknown. One of these, the fat-soluble vitamine A, is found in animal fats and in the tissues of green vegetables. If young rats are kept upon a diet lacking this vitamine, their eyes undergo a peculiar degeneration which may entirely destroy the power of vision, and the animals also fail to grow normally and finally die. Eye defects due to malnutrition occasionally develop in children, probably as a result of the lack of vitamine A.

Deficiency in another vitamine (water-soluble vitamine B) is now known to be the cause of a disease known as beriberi which is quite prevalent in countries whose people subsist largely upon a diet of polished rice. The milling methods, which remove the

outer parts of the seed, get rid of most of this vitamine. A condition resembling beriberi has been produced in pigeons fed on a diet of polished rice, but the administration of a very minute amount of vitamine B suffices to cure the abnormal condition.

The discovery of a third vitamine C has finally given the clue to the cause of scurvy. This disease was formerly much more prevalent than it is now, especially among sailors who were forced to subsist for long periods on a diet containing no fresh vegetables. It has long been known that scurvy can be prevented or cured by a diet of fresh vegetables or acid fruits, but the reason for this fact was discovered only after carefully controlled experiments on animals showed that it was due to a vitamine. Owing to the fact that vitamine C is destroyed by heat, it is not present in most canned materials.

Absence of a fourth vitamine D, formerly confused with vitamine A, produces a condition known as rickets. This disease is especially prone to attack badly nourished children, but treatment with substances rich in vitamine D, such as cod-liver oil, has been found to produce very salutary results.

Knowledge of the causes of the diseases mentioned has already been the means of saving thousands of lives and untold suffering. One cannot over-emphasize the general principle that an understanding of the normal mechanism of life processes is essential for an understanding of why the mechanism occasionally goes wrong. And if we do not understand why the mechanism goes wrong, it is only by fortunate accident that we stumble upon the means of making it go right. We shall encounter further illustrations of this fact when we consider the causes of contagious diseases.

A fifth vitamine E, discovered by Dr. H. M. Evans, has a marked influence upon the fertility of rats. Absence of this vitamine has little apparent effect upon the vitality of the animals, but it renders both the males and the females sterile. Fertility may be restored if the animals are given a small amount of green vegetables in their diet.

Little is known of the chemical composition of vitamines, or

just how they act in maintaining life. They are derived from plants, and they are required only in exceedingly minute amounts in order to perform their proper rôle.

The Inorganic Constituents. The most abundant of the inorganic ingredients of protoplasm is water. It commonly forms between fifty and seventy-five per cent of living matter. We do not look upon water as living substance, but it forms the matrix in which most of the soluble materials of living tissue are dissolved, and therefore affords a condition for most of the chemical reactions which are involved in vital activity. Both plants and animals are able to absorb water, and they frequently exhibit devices for preventing the undue loss of water through evaporation. While living tissue imbibes most of its water from the outside, water may be formed through the oxidation of the products of metabolism. Professor Babcock has shown that metabolic water, as he terms it, may be formed by many animals that are fed upon thoroughly desiccated food.

While mineral salts have long been known to occur in living tissue, it is only recently that their importance has been adequately recognized. Dr. Loeb has shown that perfectly pure water is a protoplasmic poison, since it robs the protoplasm of mineral salts which diffuse from it. He has shown that absolutely pure solutions of simple substances, such as ordinary salt (NaCl), may likewise be poisonous, but that their action may be counteracted by a small quantity of some other salt. The salt which exercises this life preservative function may itself be poisonous. The eggs of the marine fish Fundulus, put into pure sodium chloride solution of the same density as sea water, fail to develop; but if a small quantity of a salt of calcium, strontium, or even copper or lead, be added, the poisonous effect of the pure-salt solution is neutralized. These salts have an antagonistic action. A certain balance in their influence must be maintained as an essential condition of life.

Protoplasm commonly hovers on the verge between coagulation and solution, passing from the one state to the other, or

rather *toward* the one state or the other, with relative ease. It is a protean kind of stuff belonging to the group of substances known as colloids. The English chemist, Professor Graham, first clearly distinguished colloids and crystalloids. Both are soluble, but the crystalloids readily diffuse through membranes (or dialyze) while the colloids do not, or do so but slightly. There are all gradations between crystalloids and colloids, and some substances ordinarily crystalloid may occur in the colloidal state. Colloidal particles are relatively massive, and their solution has some of the properties exhibited by suspensions of very fine particles. The colloids of protoplasm readily coagulate somewhat, or pass from the sol to the gel state, when they come into contact with water, forming in this way a sort of membrane which is permeable to many substances, but which prevents the protoplasm from going into solution. Through this plasma membrane water, salts, and dissolved food materials may diffuse into the protoplasm, while other materials, the products of destructive metabolism, may diffuse out. The properties of semi-permeable membranes are of the utmost importance in biological processes. Many dead membranes are semi-permeable, allowing salt solutions to diffuse through, while they retain such substances as colloidal egg albumen. But living membranes are found to possess several properties which are different from those of dead membranes. They frequently allow substances to pass through them in one direction only; they may exhibit an electrical polarity, and their properties change under different conditions of external stimulation and with different states of the protoplasm within. It is commonly held that the outer surface of protoplasm is covered by an exceedingly thin film of a lipoid, or fatlike substance such as lecithin. The semi-permeability of living membranes has been explained as due to the presence of minute pores or spaces which would allow small molecules to pass through, but would keep out larger ones. It has been found, however, that penetrability is by no means dependent on the size of the molecules of a dissolved substance. There seems to be more probability, however, in the view of Nernst that

substances to be absorbed must be soluble in the wall or surface layer of the living cell, from which they then pass into the interior.

The films of protoplasm exhibit a considerable degree of tension, or tendency to contract. This property of surface tension is a general characteristic of physical objects, and is well illustrated in the tendency of drops of water, or of other liquids, to assume a spherical form. It is doubtless due to surface tension that fluids within protoplasm commonly take the form of spherical drops. Protoplasm appears much like an emulsion of one fluid within another. If we examine an emulsion of oil and water, or a more permanent emulsion such as milk, we observe a lot of discrete drops scattered about in a nearly homogeneous medium. If to such an emulsion a third substance is added, which tends to occupy the surface film of the liquid in which it is dissolved, the drops become surrounded by a sort of specialized membrane which tends to prevent their coalescence. This is probably what occurs in protoplasm, and gives it the character of an emulsion that is relatively permanent.

Protoplasm, as we have said, passes easily from the state of a sol to that of a gel, and vice versa, but it can coagulate only a little bit if it is able to recover its fluidity. If it passes a certain point it cannot get back, and that means death. If one makes a microscopic examination of living protoplasm which is subjected to gradually increasing temperature, the transparent material may be seen to show a whitish opacity as the thermal death point is approached. A similar change is familiar in the coagulation of the white of an egg. The assumption of a state of rigidity, or *rigor mortis*, which commonly occurs soon after death in the higher animals, is due to a coagulation of the protein of the muscles. This condition is temporary, and is followed by a stage in which the protoplasm again becomes more fluid. Very commonly death is brought about by agencies which cause protoplasm to liquefy. Normally it is prevented from going into solution by a protective, semi-permeable membrane, but if this coating is injured, the living substance may disintegrate. Micro-

scopic organisms, when injured, may frequently be seen to melt away, or dissolve, in the surrounding water, leaving only a few granules, or other contents of their living substance. In some kinds of marine flatworms the whole animal may melt away by a process of disintegration which starts in at a given point of injury and quickly spreads until it involves the destruction of the whole body.

The destructive processes which lead to death are not foreign activities imposed upon the organism. As Osterhout remarks, we should "regard the death process as a normal part of the life process, producing no disturbance unless unduly accelerated by an injurious agent which upsets the normal balance and causes injury, so that the life process comes to a standstill." Destruction and death of living tissue is a necessary element of vital activity, or, in Claude Bernard's paradoxical phrase, "La vie c'est la mort"—"Life is death." Life is maintained through a balance of constructive and destructive activities; when the latter begin to predominate, life is threatened, but there may be recovery under certain conditions which check the disintegrating agents that act on the organism. The transition between life and death is commonly a gradual one. Osterhout has found that, as death is approached, living tissue shows less and less resistance to the electric current, but after the death point is reached the resistance remains constant. He used in his experiments pieces of seaweed whose resistance to the electric current was measured by a galvanometer. When the seaweed was placed in a pure solution of sodium chloride, it was injured, and its resistance to currents and along with it the resistance to penetration by reagents decreased. After a certain amount of injury, the seaweed would more or less completely recover its normal conductivity if replaced in sea water. If the injury was slight, recovery might be complete, but if it was severe, recovery was only partial. Injury and recovery could both be subjected to definite quantitative measurements, and the influences of various substances on the vital activities of the living tissue ascertained with much precision. An accurate knowledge of the causes and

conditions of death, and how they may be controlled, is obviously of the greatest importance, for although death will overtake the protoplasm of all of us in due time, and may never be postponed beyond a certain period characteristic of our species, we are naturally desirous of circumventing it as long as we can.

Death is essentially a chemical phenomenon. The protoplasm of many forms may undergo marked physical changes, but so long as these do not entail too great a change in the chemical balance of the organism, they may not destroy life. Protoplasm is always killed by a temperature not many degrees above the boiling point of water, and usually at a much lower temperature. When it contains little water, protoplasm is more resistant to heat. The seeds of a few species of plants and the spores of some kinds of bacteria may withstand several hours of boiling and a degree of dry heat thirty to fifty degrees above the boiling point. The imbibition of water facilitates chemical changes, and it is by inducing such changes that heat produces its lethal effects.

The lower limits of temperature at which life resists destruction are exceedingly variable in different forms. Warm-blooded animals cannot stand, as a rule, a very great reduction of temperature. On the other hand, a frog may be frozen until its legs become brittle, and then recover. Fishes frozen in solid ice have often been observed to revive and swim about after the ice is melted; and hosts of aquatic insects, worms, and other small creatures, may not only be frozen, but kept for months far below the freezing point without losing the capacity to survive after they are gradually thawed out. Bacteria have been cooled down to the temperature of liquid air, and even to that of liquid hydrogen, without destroying their power of growth and multiplication. In fact, for some forms there seems to be no lower limit of temperature beyond which their life is destroyed.

Life processes can hardly be said to go on in a completely frozen organism. It is much the same with those organisms which are capable of withstanding prolonged drying. The protoplasm of beans, grains of wheat or corn, and many other seeds may become very dry and hard without impairing its capacity for

living. While the stories of the germination of seeds that were taken from the cases of Egyptian mummies have been shown to be devoid of foundation, some seeds are known to retain their vitality for many years. Among animals there are several kinds of rotifers, or wheel animalcules, and the so-called bear animalcules, or Tardigrada, which may be thoroughly dried into a mere shriveled-up mass of hardened tissue, and nevertheless regain

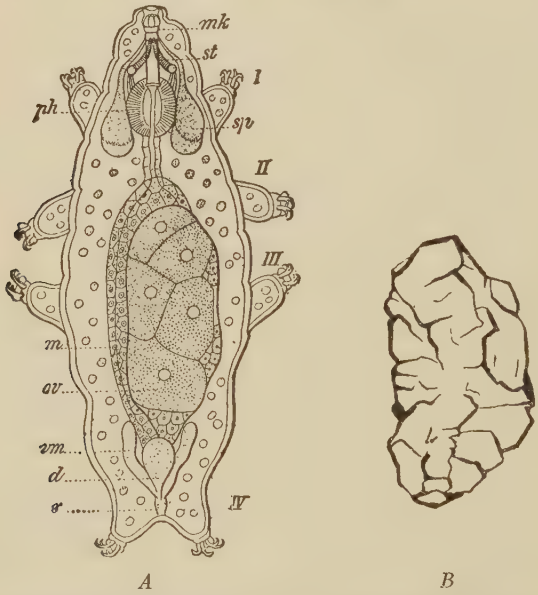

FIG. 3—A bear animalcule (Tardigrade): *A*, in the normal active state; *B*, in a dried-up condition; I–IV, appendages. (From Verworn. Courtesy Macmillan Co.)

their activity when placed again in water. This revival is all the more remarkable since these creatures have a complex organization of digestive, nervous, excretory, and muscular systems, which apparently need only to soak up water in order to function in a thoroughly efficient manner.

The life of these frozen or desiccated organisms is often spoken of as latent life. Metabolism probably does not go on at all at the temperature of liquid air, and it goes on very slowly in a desiccated seed or animalcule, for even dried seeds have been

shown to give off a very slight amount of carbon dioxide. With cooling and drying, chemical changes gradually cease. Whether we say that life in these forms was destroyed and later resumed, or whether we call their life latent, or suspended, is largely dependent on how we define our terms—a question of words rather than one of fact.

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CHAPTER III

THE CELL, CELL DIVISION, AND THE CELL THEORY

The protoplasm of all higher plants and animals is organized into minute units called cells. Whether we study the microscopic structure of the wood, bark, and leaves of a tree, or that of the muscles, glands, bones, or brains of an animal, what we encounter is a multitude of these cellular units. Higher organisms are composed of cells much as a brick house is composed of bricks. This is a somewhat bald statement of the celebrated cell theory, although, as thus formulated, it cannot be said that there is anything theoretical about it at the present time. It is simply a generalized statement of observed facts. From the standpoint of this doctrine, the cell is a unit of composition modified in different ways in relation to the discharge of different functions. To a certain degree the cell has an individuality of its own, while its form and activities are subordinated to the needs of the whole body. The conception of an organism as composed of cells has played a very important part in the development of biology, although this fruitful generalization is a product of relatively recent times.

The discovery of cells had to wait upon the perfection of the microscope, which made possible the revelation of structures hitherto hidden from the eyes of man. The first clear description of cells was given by that versatile genius, Robert Hooke, who observed in 1665 that cork is composed of "little cells or boxes." Hooke saw only the walls of the cells after their living contents had disappeared, and quite naturally he regarded the cell wall as the essential feature of the cell. The name which he employed, however inappropriate it may be in the light of more recent knowledge, still persists. Cells were soon afterward

described in various kinds of plant tissues by the English botanist, Nehemiah Grew (1672), and in both plants and animals by the Italian anatomist, M. Malpighi, the latter regarding the cell as a kind of unit with its own wall, or utriculus. In 1833 Robert Brown observed in many kinds of plant cells a rounded body, which he called the nucleus, and which contains a very much smaller body, the nucleolus. Although many contributions to our knowledge of the cell, and its rôle in physiology and development, were made by Martin Barry, C. F. Wolff, Leeuwenhoek, Meyen, and Treviranus, the credit for the formulation of the cell theory is usually given to two German investigators, Schleiden and Schwann, whose first writings on the subject were published in 1838 and 1839. These investigators recognized the cell as consisting typically of a cell wall and its contained living substance, inclosing a nucleus. In 1846 this living substance was designated as protoplasm by von Mohl who employed a term previously used by Purkinje in a somewhat different sense. Schleiden and Schwann laid much stress on the wall as an essential constituent of the cell, but the discovery of cells in which a definite cell wall is absent, led to a modification of this conception. As Max Schulze defined it in 1861, a cell is "a bit of living protoplasm containing a nucleus."

Inasmuch as the growth and development of an organism involve an increase in the number of its cells, the attention of the earlier investigators was naturally directed to the problem of how new cells arise. Schleiden and Schwann both held that new cells arise by a sort of condensation of living material from a fluid matrix, the nucleolus forming first, then the nucleus, and finally the surrounding protoplasm with its cell wall. New cells were supposed to form within old cells, or at times, according to Schwann, in the nutrient fluid outside the cells entirely; but the labors of subsequent investigators corrected these errors and showed that new cells are furnished by a division of other cells, a conclusion that was formulated by Virchow in his famous aphorism, "*Omnis cellula e cellula.*" Later it was established that the nucleus of each cell arises by a division of the nucleus of the

parent cell (*Omnis nucleus e nucleo*). The later developments of the cell theory thus lead us to regard a plant or animal as a sort of aggregation of cells, each of which has arisen by the division of preëxisting cells. It was inevitable, therefore, that the cell theory should exert a profound influence upon our conceptions of embryonic development and the whole subject of the perpetuation of life. Schwann showed that the ovum, or egg, which forms the starting point of the development of the individual organism, consists of a single cell. Later the spermatozoön by which the egg is fertilized and stimulated to develop, was shown to be also a single cell, although one of very much smaller size. It soon came to be recognized that the development of the individual from the fertilized egg is brought about by the division of cells, their growth and differentiation, and their orderly arrangement. The physiologist may look upon the functioning of the body as a series of coördinated activities of the numerous little cellular units of which it is composed. Whether we are walking, thinking, or quietly digesting our food, we may regard ourselves as a great congeries of multitudinous little individualities, all performing their several tasks in our muscular, nervous, digestive, and other systems of organs. An organism is analogous to a society whose individual members coöperate in the various activities of social life, and the phrase "cell state" is often employed to point out a fundamental likeness between organic and social activities.

It should be clear, I think, that a proper understanding of fundamental life processes involves an acquaintance with the organization and activities of cells. Let us look, then, at the make-up of a typical cell, which we find to be much as follows: Surrounding the whole is a cell wall, which, in plant cells, usually consists of a carbohydrate called cellulose, which is to be regarded as a product formed by the living protoplasm; in the animal cell the wall is a specialized protoplasmic layer. There are many cells of animals and some cells of plants which are devoid of a permanent surrounding membrane. The protoplasm outside the nucleus is now designated as cytoplasm, and it

exhibits the structure described in the last chapter. In the alveoli of the protoplasmic network, or foam work, there is contained the more fluid cell sap, or other inclusions, such as fat or yolk. In addition to the granules previously described, there may be seen in many cells a minute rounded body called the centrosome, often surrounded by a rounded mass of cyto-

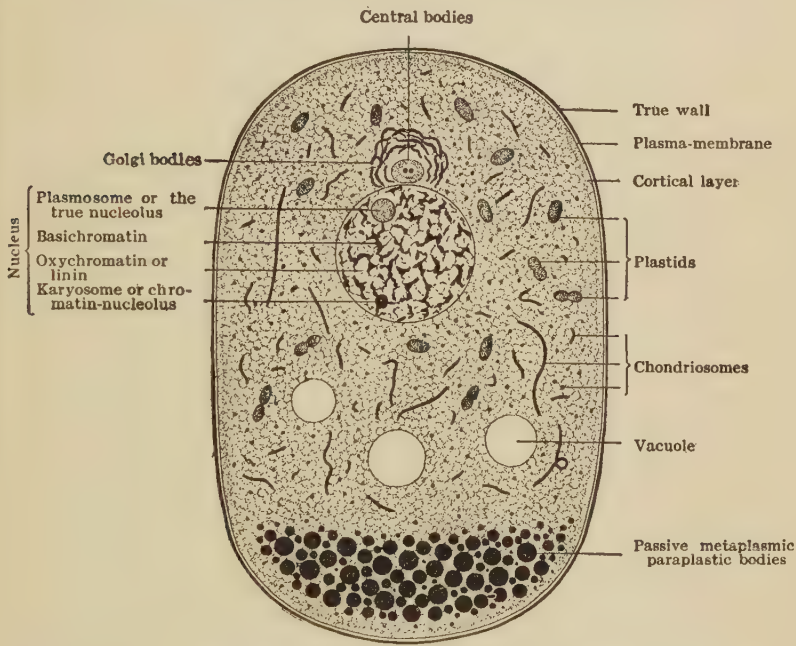

FIG. 4—A typical cell. The cytoplasm, or protoplasm surrounding the nucleus, appears in the form of a network, or foam-work, containing various other bodies. (From Wilson's *The Cell*. Courtesy Macmillan Co.)

plasm, known as the attraction sphere. Both of these bodies play an important part in cell division, and the centrosome, since it commonly arises by division from a preceding centrosome, has often been regarded as a distinct and permanent cell organ. In exceptional cases, however, it has been proven that the centrosome may arise *de novo*. In plant cells especially there are small refractive bodies, the plastids, which often exhibit the power of multiplication by fission. These bodies are associated

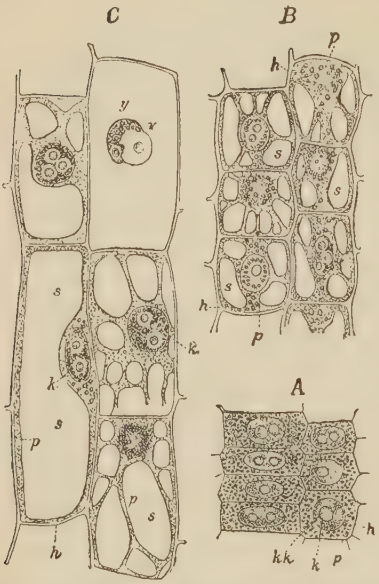

FIG. 5.—Cells from the root of Fritillaria: *A*, young cells filled with protoplasm; *B*, older cells showing vacuoles, or spaces filled with sap, *s*; *C*, still older cells with larger vacuoles; *h*, cell wall; *k*, nucleus; *kk*, nucleolus; *p*, protoplasm. (After Sachs.)

with the formation of starch, chlorophyll, and other cytoplasmic products of the plant cell.

Recently much attention has been devoted to a class of bodies called chondriosomes. These frequently appear in the form of threads, which may be demonstrated in the cytoplasm by the use of appropriate stains. In some cases these threads divide with the division of the cell. There may be still other bodies which divide and thus perpetuate themselves, and it has been conjectured that the minute microsomes which occur in the protoplasmic network, also have this property, but this has not been established.

The nucleus of the cell is generally spherical, and inclosed in a distinct nuclear membrane. The framework of the nucleus consists of a substance called

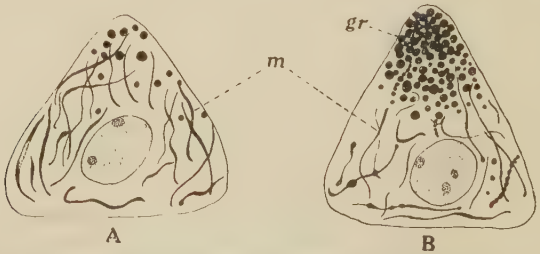

FIG. 6.—Chondriosomes in cells from the pancreas of the rabbit: *A*, cell in resting state; *B*, in active state; *gr*, granules of secretion; *m*, chondriosomes (mitochondria). (After Hoven.)

linin, which frequently appears as a network, or framework resembling that of the cytoplasm. The interspaces of this network

contain a fluid called nuclear sap. In most nuclei there is a small rounded body (rarely two or more) called the nucleolus (plasmosome), which in certain dyes is colored differently from the surrounding structures. Although several theories have been advanced as to the function of the nucleolus, the significance of this little organ remains a complete enigma.

The most important and distinctive substance in the nucleus is the chromatin, so called on account of its property of taking up many coloring matters which are commonly employed in the study of the cell. Chromatin generally occurs as granules or lumps scattered about on the linin network, and it appears to be essentially granular in composition. Sometimes a part of this

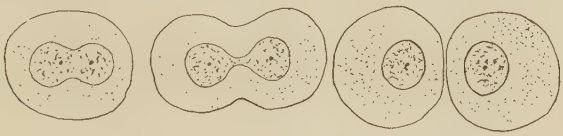

Fig. 7—Stages of direct, or amitotic cell division.

substance may be aggregated into a mass called the chromatin nucleolus, or karyosome. Chemically, chromatin belongs to the nucleo-proteins, a class of compounds distinguished, among other things, by the possession of phosphorus. The chemical composition of chromatin probably changes under different conditions, as is indicated by its varied reactions to stains. Much interest attaches to this chromatin, as will be seen later.

For some time after the establishment of the fact that cells always arise by the division of other cells, it was held that cell division occurs by the constriction of the nucleus and nucleolus into two parts, followed by a similar fission of the cytoplasm. This process, which is known as direct cell division, or amitosis, sometimes occurs, but it is an exceptional procedure, and is apt to take place in cells which are abnormal or destined to live only a short time.

The modern student of the cell has a great advantage over the investigators of a half-century ago. He is able to employ microscopes of wonderful efficiency in giving very high magni-

fication, combined with remarkable clearness of definition. Through perfecting the arts of fixing and staining tissues, and the cutting of very thin sections, he has learned much of the technique of preparing materials for examination, and he has thus been able to make observations which were impossible for his predecessors. One of the most striking of the discoveries that have been made in regard to the cell is the revelation of the real method by which cells usually divide. This is the method of mitosis (karyokinesis), or indirect cell division. Mitosis is commonly initiated by the division of the centrosome and its surrounding sphere, or by the division of the latter alone when a centrosome is not present. The two centers separate more and more widely, and from each what appear to be fibers radiate into the surrounding cytoplasm. Each of these centers with its rays is called an aster, from its resemblance to a star, and its radiating strands are known as astral rays. As the asters separate, a clear, spindle-shaped body develops between them and appears to be traversed by fibers which converge toward the poles. The more widely the asters are separated, the larger they become and the longer is the spindle which connects them. Finally they come to lie on the opposite sides of the nucleus, but usually before this has occurred the nuclear wall has broken down and other changes have taken place which have effected a remarkable transformation of the nuclear contents.

Mitosis involves parallel series of changes within and without the nucleus, which seem to work together in a kind of "pre-established harmony." In the very early stages of the process, and often before any external signs of division are visible, the chromatin of the nucleus aggregates into the form of threads, and not infrequently into what appears to be a single coiled thread. This is the so-called spireme stage, and it is followed by a stage in which the chromatin is in the form of separate threads or rods, called chromosomes. When the nuclear membrane breaks down, the chromosomes are fully formed and are ready to take their place on the spindle. Now comes the bringing together of the two processes involving the chromatin on the

one hand and the achromatic apparatus of asters, spindle, etc., on the other. The chromosomes are drawn upon the spindle, forming a ring around it; frequently they are in the form of V's, with their apices toward the center of the figure. Each chromosome undergoes a longitudinal splitting, if it has not already done so before this stage, and the two halves, or daughter chromosomes, are pulled toward their respective poles. Some of the rays of the aster are apparently attached to the chromosomes, and it seems not improbable that they have something to do with pulling the chromosomes apart. As the chromosomes approach the poles of the spindle they become vacuolated, lose their regularity of outline, and become converted into new daughter-nuclei. In the meantime the cytoplasm becomes divided, and thus completes the division of the cell. The nucleolus, which discreetly disappeared in all this turmoil, is replaced—but how, we do not know—by a new nucleolus in each of the daughter-nuclei. In the later phases of mitosis, the spindle, asters, etc., gradually vanish (Fig. 8).

Such is the ordinary method of cell division. The precise way in which the indirect division of the cell is carried out varies somewhat in different forms. In most animal cells division is effected by a constriction of the cytoplasm. In the plants the cells generally do not constrict, but a cellulose plate develops at right angles to the middle of the spindle and forms a double cell wall. This plate develops in close association with a series of granular thickenings, which occur across the middle of the spindle fibers. In many one-celled organisms, and in some higher ones, the spindle forms inside the nucleus. It is among the primitive organisms that we meet with the widest departures from the typical method of mitosis, and several intermediate stages are found between simple amitotic fission and the complex type we have described. Apparently an elaborate mechanism of division was perfected very early in the evolution of life. How many mitotic divisions have succeeded one another without serious mishap during the course of evolution, we can only vaguely conjecture.

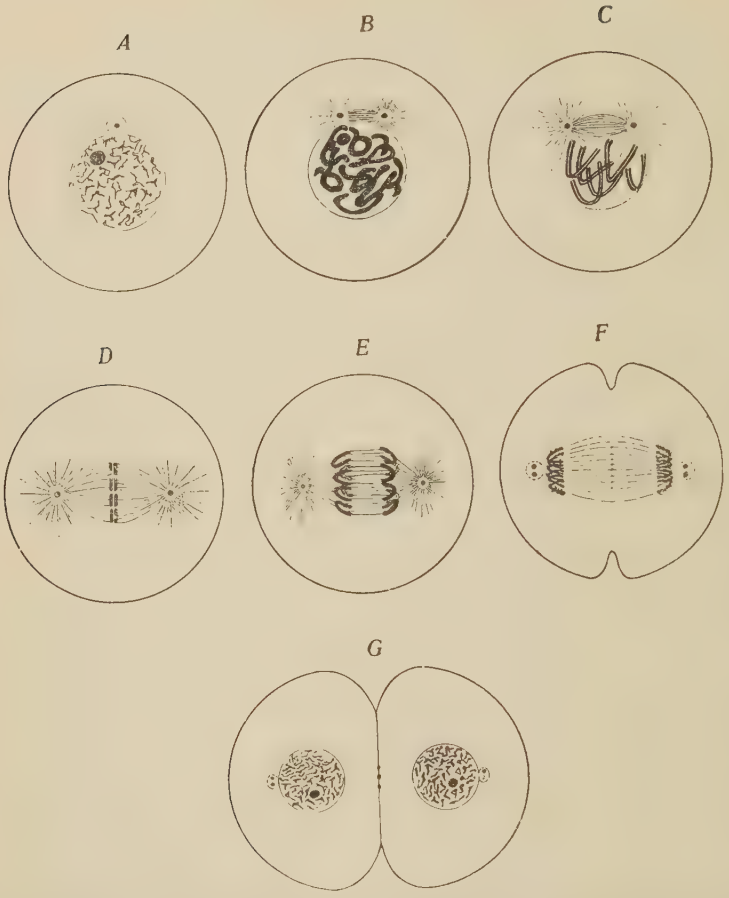

FIG. 8.—Diagram of successive stages of mitotic cell division. *A*, resting cell with centrosomes lying near the nucleus; *B*, the chromatin of the nucleus is in the form of chromosomes, and the centrosomes have divided and are surrounded by short astral rays and are connected by spindle fibers; *C* shows a larger spindle; the nuclear membrane is breaking down and each of the chromosomes shows a longitudinal split. In *D* the nuclear membrane has disappeared, the chromosomes are arranged around the central part of the spindle. *E* shows the halves of the split chromosomes being drawn apart toward the poles of the spindle. In *F* the chromosomes, which are pulled still farther apart, begin to show an irregular outline, and the cytoplasm is being constricted into two parts. *G*, the end stage, in which cell division is complete and the nucleus of each daughter cell is in the resting stage. The centrosomes have divided in preparation for the next cell division.

It must be admitted that our efforts to throw light on the mechanism of mitosis have not yet been fraught with much success. The process involves the calling into operation of an elaborate cytoplasmic mechanism, which appears to come into existence, as it were, out of a clear sky. It involves, also, a parallel formation of definite chromosomes out of the resting reticulum of the nucleus, their orderly deployment, like soldiers of a well disciplined army, their precise division, and finally their

FIG. 9—Group of cells from the growing root tip of the onion showing various stages in the mitotic division of the cells. *s*, spireme; *m*, *a*, *t*, successive stages of mitosis. (From Wilson. Courtesy Macmillan Co.)

conversion into a new resting nucleus. There is nothing in the appearance of an ordinary cell which gives any indication of its capacity for such an amazing performance. It has been pointed out that the process of mitosis affords a means of precisely dividing the constituents of the cell, and especially the chromosomes. When we come to consider the problems of heredity and development, we shall find that this is a very useful thing to have accomplished, but pointing out the use of a process is a teleological interpretation and does not give us the least information about the causes by which the result is achieved. An explanation of simple amitotic division in terms of known principles,

might not seem so staggering a task, but when it comes to the complex mechanism of mitosis, we may well share the feeling of Professor Bateson, who says: "I know nothing which, to a man well trained in scientific knowledge and method, brings so vivid a realization of our ignorance of the nature of life as the mystery of cell division. . . . It is this power of spontaneous division which most sharply distinguishes the living from the non-living. . . . The greatest advance I can conceive in biology would be the discovery of the instability which leads to the continued division of the cell. When I look at a dividing cell, I feel as an astronomer might if he beheld the formation of a double star: that an original act of creation is taking place before me."

Cell division, like other forms of reproduction, is intimately associated with growth, and growth, owing to the simple geometrical principle that the surface of a body increases as the square of its diameter, while the volume increases as the cube, brings about a disproportion between surface and volume. A more nearly normal balance would therefore be restored by division, but this is a mere statement of the utility of division and gives us no real insight into its cause.

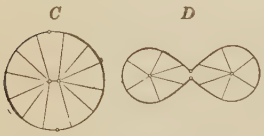

FIG. 10—Apparatus to illustrate mitotic cell division. *C* shows the small rings near the center connected by a strand. *D* represents the form assumed after this strand is cut, the elastic bands extending from the periphery to the small central rings have pulled the rings farther apart and have strongly constricted the outer margin of the figure. (After Heidenhain.)

There have been many attempts to explain the formation and workings of the mitotic figure. Heidenhain has constructed an ingenious mechanical model, consisting of two half-rings of flexible steel, joined by hinges and furnished with several rubber bands which extend from the periphery to a pair of small conjoined rings in the center (Fig. 10). The bands correspond to the astral rays; the small rings, to the centrosomes; the half-rings of steel, to the cell wall; and the band connecting the rings, to the spindle. If the band connecting the small rings be cut, the contraction of the rubber bands pulls the centers apart and causes the half-rings

to close in, so that each forms a complete ring. A contractile function has often been ascribed to the astral rays. Some of them, whatever they may be, have been observed to become attached to the chromosomes, and the substance of the chromosome has occasionally been seen to be pulled out a little where the ray is inserted.

Ziegler, Gallardo, and others, assume that the centrosomes are the seat of attractive forces which pull the chromosomes apart. There is a rather striking resemblance between the mitotic figure and the lines formed by the arrangement of iron filings in a magnetic field. Sprinkle iron filings upon a piece of cardboard and hold it over the poles of a magnet, and you will see the filings arranging themselves between the poles in a way that resembles a spindle, and radiating from the poles like the rays of the aster. It is not improbable that electro-magnetic forces play a part in cell division, and it has been suggested that the spheres and centrosomes are electrically charged bodies which exert an attractive force upon the oppositely charged chromosomes.

A most promising line of attack upon the problem has been made by the methods of micro-dissection which have recently been carried to a high state of precision. The tissue to be dissected is placed in a hanging drop of fluid on the lower side of a thin slip of glass, the whole being kept in a moist chamber to prevent evaporation. By means of glass needles drawn out to an extreme fineness and operated by a system of screws so as to permit of slow and accurately adjusted movements, it has been found possible to operate on the living cell while it is being observed under the highest powers of the microscope. In a resting egg cell the needle may be moved about quite freely without encountering much resistance, thus showing that the cytoplasm is in a fluid state. The nucleus in such a cell may be pushed about like a rubber ball, and it may even be dissected and its chromosomes in the spireme stage pulled out as long elastic threads. Dr. Chambers, who has carried the technique of micro-dissection to a high degree of refinement, is able to poke

about the different parts of the mitotic figure almost at will and to ascertain their consistency. He finds that the spindle is at first a jellylike body with considerable firmness, but that in later stages of mitosis it tends to liquefy. To how great an extent the growth of the spindle tends to push the centrosomes apart is not entirely clear. The asters are relatively solid bodies, but the clear matter immediately around the centrosomes appears to be fluid and offers no resistance to the movements of the needle. The material immediately surrounding this clear area is the firmest region, and the consistency of the aster becomes more fluid toward the periphery. To all appearances the rays are of the same substance as the clear area, and fluid in consistency. As the asters enlarge, material appears to flow into the clear area along the astral rays. At the periphery the cell is more liquefied. The gelation setting in at the two poles of the spindle, which is at its maximum at the time of the greatest development of the aster, is apparently concerned with causing the cytoplasm to become more and more constricted at the middle region of the dividing cell where it is more fluid in consistency. As the asters disappear at the close of mitosis they lose their firmness, and the contents of the cell assume again a more nearly liquid state. The chromosomes may possibly be pulled apart by the currents which flow toward the centers along the channels indicated by the appearance of the astral rays.

Micro-dissection experiments have changed some of our prevalent interpretations of the phenomena observed in mitosis. They have shown that the changes of colloidal protoplasm from the sol to the gel state and vice versa play an important part in effecting the division of the cell, and they promise to throw still more light on the real mechanism of this wonderful procedure.

Of all the constituents of the cell the chromosomes have received by far the largest amount of attention at the hand of modern cytologists. This is largely due to the part which chromosomes are held to play in reproduction and hereditary transmission. The older students of the cell had no suspicion of their existence. But now that their great theoretical significance

is coming to be revealed, they promise to become as familiar topics of conversation as bacteria or X-rays. It is a general rule that each species of organism has its characteristic number of chromosomes. They vary in number from two in a species of parasitic worm (*Ascaris megalocephala* var. *univalens*) to considerably over a hundred. The number in man is probably forty-eight. In the sweet pea there are fourteen; in the common fruit fly, eight. Since the number of chromosomes in each species is generally constant, the question arises, Do these bodies represent individual, self-perpetuating entities, or is their constancy in number a result of their development *de novo* from the same kind of material? Men normally have the same number of fingers, toes, ribs and teeth, but no one considers that these structures are handed on, as continuous organs, from one generation to the next. The constancy in the number of chromosomes might plausibly be explained in somewhat the same way, but there has accumulated a very convincing body of evidence that these little organs actually retain their individuality through the resting stages of the nucleus. Not only do chromosomes retain their characteristic number, but there are frequently also peculiarities of size and shape which constantly reappear after successive cell divisions. Where an abnormal number of chromosomes has been produced, this also is perpetuated, and in the cells of hybrid organisms it is generally possible to distinguish the chromosomes characteristic of both parental species. In exceptional cases, indications of persistent chromosome pockets may be seen in the resting nucleus, and in the fish Fundulus, Richards has shown that the chromosomes at the end of cell division do not fuse together, but each swells up to form a sort of little nucleus of its own. It seems reasonable to suppose that what happens in the ordinary resting nucleus is that the vacuolated chromosomes become so closely packed together that it is no longer possible to discern their boundaries, and that when the chromosomes emerge again for the next division they are constituted of the same material as before.

The evidence of chromosome individuality derived from the

study of cytology is strongly supported by independent evidence derived from the study of heredity. Among both cytologists and geneticists there is a widespread acceptance of the dictum, *Omnis chromosoma e chromosoma*. In several organisms there is evidence that the chromosomes are composed of smaller components often appearing like granules and known as chromomeres. In the longitudinal splitting of the chromosomes in mitosis each chromomere appears to divide, so it is not improbable that these smaller units are self-perpetuating individualities also. Here again we have observations of the greatest interest in relation to the facts and theories of heredity, as will be seen in a later chapter.

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CHAPTER IV

THE TISSUES AND THEIR FUNCTIONS

It might naturally be inferred that higher organisms are composed of many different kinds of cells. Complicated biological mechanisms like ourselves with our varied activities of digesting, absorbing, eliminating, moving about, and thinking, require many kinds of cellular units. And these different kinds of units are intimately related to the number of different things which our bodies can do. We have specialized muscle cells through the contraction of which we execute our numerous movements; secretory cells which aid in digesting our food; other cells which absorb the digested products; and nerve cells which are concerned in conducting stimuli, and in thinking, which involves a special and highly elaborate kind of conduction of stimuli. We cannot get very far in understanding either the structural make-up or the workings of an organic body without becoming acquainted with its different kinds of cells.

Cells in all complex organisms are massed together into groups called tissues, the knowledge of which constitutes the subject-matter of the science of histology. In the animal body the kinds of tissues generally distinguished are epithelial, connective, muscular, and nervous, some writers adding blood and lymph as a separate variety. Epithelium is a very common type of tissue in which the cells are arranged in layers. These layers may be one or more cells thick, and the cells are usually polyhedral in outline as the result of mutual pressure. Sometimes epithelium consists of much flattened cells (squamous epithelium), as in the shed outer skin of the frog and the outer cuticular cells of our own skin. Epithelial cells are sometimes cuboidal, or more frequently columnar in shape. In the variety called ciliated epithelium the exposed surface is furnished with

numerous hairlike processes called cilia which rapidly beat to and fro, thus creating a current in the fluid by which the cells are bathed. The currents caused by cilia frequently carry off foreign particles, as is the case with the lining epithelium of our windpipe. Clams, oysters, and a host of other marine animals get their living by the industrious beating of the ciliary epithelium which carries to the mouth the small organisms which these creatures utilize for food. The currents created by the cilia on the gills of molluscs and other animals aid in the process of respiration; in some cases these currents carry the products of elimination to the

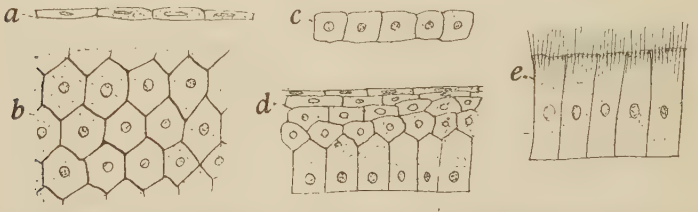

FIG. 11—Varieties of epithelium: *a*, *b*, flattened, or squamous epithelium, the cells seen from the side in *a*, and from above in *b*; *c*, cuboidal epithelium; *d*, epithelium several cells in thickness—the deepest cells are columnar, but the others become more flattened as they are pushed outward; *e*, columnar ciliated epithelium.

outside of the body. In some animals, especially in the larval state, cilia afford the means of swimming through the water. The beating of cilia is worked in to perform a variety of useful functions; in fact most animals which have cilia are dependent upon them for their life.

Epithelium is a kind of covering tissue used for lining various organs both within and without. In our own bodies it not only covers the entire outer surface, but forms the inner layer of the alimentary canal and all the glands attached thereto. Epithelium lines the body cavity and the organs which project into it, such as the liver, kidneys, and pancreas. It coats the heart and the blood vessels inside and out, and constitutes the secreting cells of glands which discharge their contents through a duct. In almost every place where there is an exposed surface there is a coating of this tissue.

Epithelium performs a variety of functions. It is frequently

modified for the purpose of absorption, as in a considerable part of the intestine. It is the tissue usually involved in secretion, which is its function in the glands of the stomach and intestine, and the tubules of the liver, kidneys, and pancreas. In some places it is sensory in function, as in the olfactory epithelium of the nasal cavities and the auditory epithelium of the inner ear. In many animals it subserves the function of reproduction in giving rise to the sex cells.

In stratified epithelium, where there are several layers of cells, the new cells are formed in the deeper layers and gradually become pushed toward the periphery as they get older. As they pass outward, the cells become thinner and flatter, and in the outer skin they become dead, dried, and corneous and are finally cast off. In those animals which we speak of as shedding their skin, the whole outer cuticle may be cast off in a single intact layer, as in snakes; in the frog the cuticle comes off in large pieces, while in mammals the outer dead cells are shed gradually and unobtrusively in much smaller masses. In all these forms the cells are actively renewed in the deeper layers, and are gradually pushed outward, to die and be cast away (Fig. 11).

Epithelial cells are closely fitted together, each cell being separated from its neighbors by a thin film of what is called intercellular cement substance. Sometimes this substance appears to be crossed by strands which have been considered to be protoplasmic bridges connecting one cell with another. The cells of epithelium form continuous sheets in which there are normally no gaps; and if on account of injury a surface becomes denuded of its epithelial coating the latter is quickly regenerated. This covering of exposed surfaces results not merely from the formation of new cells, but more from the fact that epithelial cells creep over the surface from neighboring areas. These cells are not like so many passive building stones, as we might be prone to consider them; they are like active organisms endowed with the power of movement and response to stimulation. This property has been demonstrated by growing these cells outside the body and observing their behavior. The method of growing

tissues outside the body was perfected a few years ago by Harrison, Carrel, and others, and it has made possible the discovery of many interesting facts. The tissue to be studied is placed in a hanging drop of blood plasma or other suitable medium suspended on the lower surface of a thin cover glass over the cavity of a hollow glass slide.

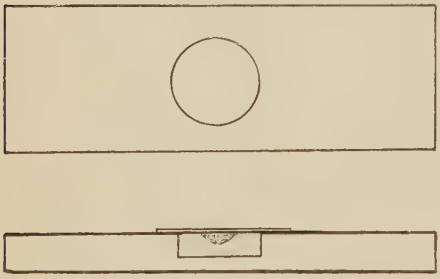

FIG. 12—A hollow glass slide seen from above in the upper figure and from the side in the lower one. The lower figure shows a drop of culture fluid hanging from the cover slip over the central cavity.

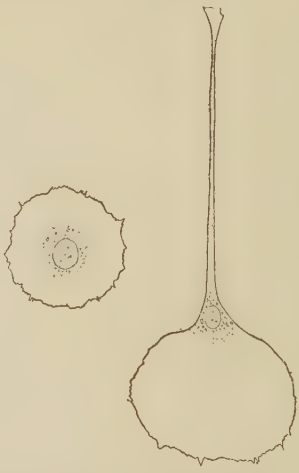

FIG. 13 — Cells of epithelium grown in an artificial culture medium. One cell shows a long process which has been drawn out by the amœboid movement of the protoplasm.

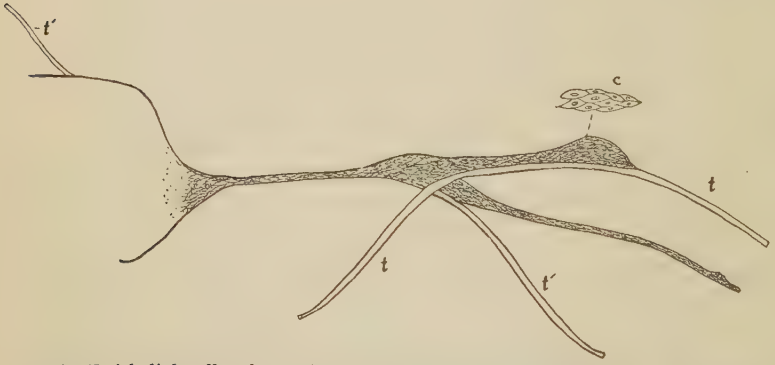

FIG. 14—Epithelial cells of a tadpole cultivated in a hanging drop. Strands of cells have crept out along fibers of cotton wool, *t*, *t*; *c*, a group of cells more highly magnified.

It is thus possible to observe the tissue with a microscope and follow its changes. If one prepares in this way a bit of epithelium

from the skin of a frog, or better, a tadpole, the cells may be seen to creep out from the margin of the tissue as a very thin sheet which actively extends over all available solid objects with which it comes in contact. Bits of sterile cotton fibers or other objects put in contact with epithelium may receive a complete coating of this tissue. In fact, epithelium exhibits a remarkable proclivity to spread over all sorts of surfaces. It is doubtless owing in large part to this peculiar trait of its behavior that epithelium is so generally distributed as an investing layer over so many surfaces of bodily organs.

FIG. 15—Fibrous connective tissue showing cells amid the fibers.

In connective tissue the cells are separated by a matrix of supporting substance which is usually much greater in bulk than the cells themselves. The general function of connective tissue is to bind together and sustain the parts of the body. In white fibrous tissue there is a clear matrix in the form of a layer, or often a spongy network, containing fibers which give it strength. Scattered about in the matrix are cells which are generally irreg-

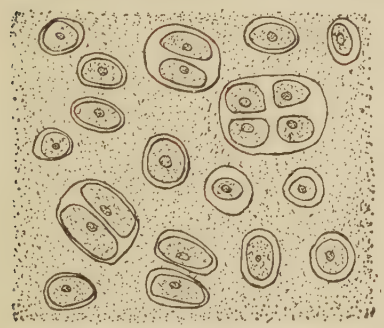

FIG. 16—Cartilage showing the cells lying in spaces within the matrix. The paired arrangement of some of the cells is the product of recent cell division.

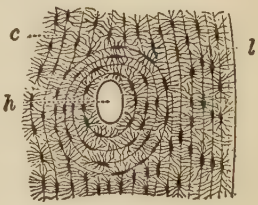

FIG. 17—Microscopic structure of bone: *c*, the bone cell; *h*, a Haversian canal, or channel, containing blood vessels; *l*, the lamellæ, or layers of bone formed by successive stages of growth. (After Hatschek.)

ular in form. This white fibrous tissue forms a framework as well as an outer covering for most organs. A very tough and inelastic form of it occurs in tendons and ligaments. Cartilage is a connective tissue in which cells are imbedded in a tough, usually transparent, intercellular substance. In bone, the intercellular substance is hardened by the deposit of lime salts, mainly phosphate of lime.

Muscular tissue consists of cells which are specialized in relation to the function of contraction. Two chief varieties are distinguished, the non-striated and the striated. The former consists of cells usually spindle-shaped, occasionally branched, and containing a single nucleus. Unstriated muscle is often designated as involuntary, since its action is not directly subject to voluntary control. It occurs in the coats of the stomach and intestine, the ducts of various organs, and the walls of blood vessels. Its contraction is relatively slow, like its subsequent relaxation, and it is accordingly not well adapted to execute the prompt reactions which are often called for in making adjustments to the happenings of the outer world.

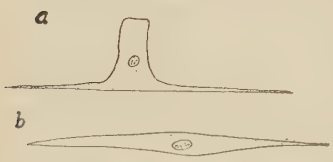

FIG. 18—*a*, an epithelio-muscular cell; *b*, a fiber of non-striated muscle.

What is commonly called behavior in the higher animals, is mainly a result of the contraction of the fibers of striated, or voluntary muscle, although not all the contractions of striated muscle are under the control of the will. Our skeletal muscles—those which move our limbs, head, and trunk—are of the striated variety, and it is probably owing to the quick actions which they are called upon to perform that the fibers show a degree of structural differentiation much exceeding that of non-striated muscle. The cells are elongated, relatively large in size, and surrounded by a distinct cell wall, the sarcolemma. In the higher animals there are often several nuclei in each fiber. The

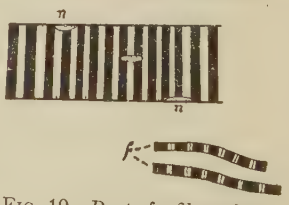

FIG. 19—Part of a fiber of striated muscle: *n*, nucleus; *f*, individual fibrillæ.

protoplasm of the cell contains a large number of parallel strands, the fibrillæ, which are differentiated at regular intervals of their course so as to give rise to the appearance of transverse bands, or cross striations. Between the fibrillæ, the protoplasm is of relatively fluid consistency. These fibrillæ are considered to be the contractile elements, since they may be seen to shorten and thicken and also to undergo certain optical changes as the muscle contracts.

Contractility is a general property of living matter which is greatly exaggerated in specialized muscular tissue, and many theories have been advanced to explain it. It has been suggested that it may be due to an increase in the surface tension of the fibrillæ, but more recently contraction has been affiliated with the phenomenon of gelation, which is a common trait of colloidal substances. Muscular work involves chemical changes, and the energy for its production comes mainly from the decomposition of carbohydrates present in muscular tissue. Contraction is accompanied by the formation of lactic acid, phosphates, and CO_2, and these (or other) substances may affect the fibrils in such a way as to cause them to shorten. The cause of muscular movement is still an unsolved problem, but it is not improbable that it has a fundamental relation to the cause of amœboid movement and the beating of cilia, different though these phenomena appear superficially to be.

Nervous tissue consists of nerve, or ganglion, cells and nerve fibers. What we call nerves are usually bundles of nerve fibers which extend from some center such as the brain or spinal cord. In the medullated nerve fibers there are distinguishable (1) an outer thin sheet (neurilemma) within which is (2) a layer of fatty substance called myelin forming the medullary sheath, and (3) a central axis cylinder which is the real conducting part of the fiber. The axis cylinder is always connected with, and is in fact an outgrowth of a nerve cell, the surrounding sheaths being of extraneous origin, and serving as protecting or possibly insulating coats. In the non-medullated fibers the myelin sheath is dispensed with, and the axis cylinders have a thin, connective

tissue covering, and even the latter is not infrequently lacking, especially toward the end of the fiber.

Nerve cells are exceedingly variable in size and shape. Usually they are provided with a number of branching processes, or dendrites. In those cells from which nerve fibers take their origin a single unbranched process, or axon, passes out to form the cen-

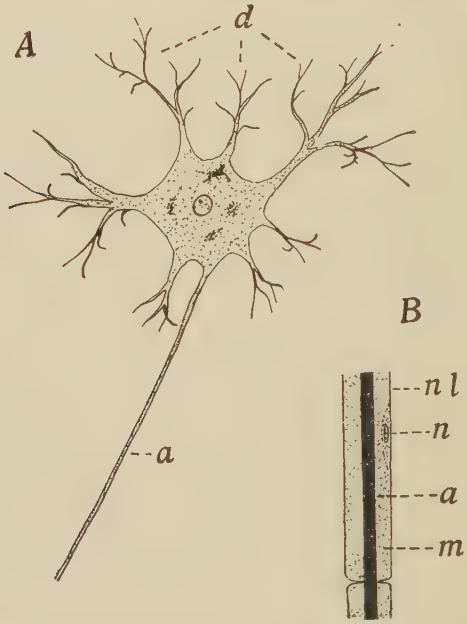

FIG. 20—*A*, nerve cell; *B*, part of a medullated nerve fiber; *a*, axis cylinder; *d*, dendrites; *m*, medullary substance; *n*, nucleus; *nl*, neurilemma.

tral core, or axis cylinder, of the fiber. In the cytoplasm of the nerve cell and its branches there occur numerous very fine fibrillæ which usually run in several directions in the body of the cell, but take on a parallel course in the dendrites and axis cylinders. It has been conjectured that these fibrils are especially concerned in the conduction of impulses.

As muscle cells are specialized in relation to the function of contraction, so nerve cells and their fibers are specialized in relation to the conduction of stimuli, but conduction, like con-

traction, is a general function of protoplasm, and is exhibited to a certain extent by all cells of the body. The cellular units of the nervous system, or neurons, are connected in such a way that impulses are carried from one to another. In lower animals the branches of the adjacent nerve cells appear to be actually confluent so as to form a perfectly continuous nervous network. In the higher animals, on the other hand, the processes of the nerve cells come into intimate contact, but are separated by an exceedingly thin membranous partition called the synapse, across which the nervous impulse, however, is able to pass. Neurons are arranged into a highly elaborate system of connections by which any part of the body is put into relation with practically any and every other part. Impulses may be carried from the sense organs to the nerve centers, whence they may pass outward so as to invoke a response in some other organ. The nerve center is furnished with a number of different possible lines which the impulse may take in a manner more or less analogous to the central office of a large telephone system which has the possibility of connecting John Smith with any of the persons listed in the telephone directory. Now nerve impulses are the occasion of the contraction of muscles, the secretion of glands, and other organic activities; hence their transfer and proper coördination is essential to the orderly regulation of reactions which is required for successful living.

But what is the nature of the impulse which the nerve fibers transmit? It has been thought to be an electrical change such as passes over a wire when we use the telephone or telegraph. It has in fact been demonstrated that electrical changes accompany the nerve impulse, but this fact in itself does not prove that nerve transmission is essentially the same as the passage of an electrical current through a wire. In the first place, the nerve impulse travels very much more slowly than the electric current, its rate being in mammals roughly 129 meters per second. In the cold-blooded frog its rate is only 29.7 meters per second, and in some of the lower invertebrate animals it has been found to be very much slower still. A widely accepted view

at present is that the nerve impulse consists of a wave of chemical change which might be compared with the transmission of an explosion along a train of gunpowder, although, unlike the gunpowder, the nerve fiber has the property of quickly recovering its labile condition. According to the chemical theory the electrical changes which accompany the nerve impulse might easily be accounted for, since chemical changes involve the transfer of electricity. It has been found difficult, however, to detect the chemical changes occurring in a nerve. For a long time it was impossible to prove that a stimulated nerve gives off more carbon dioxide than it does when at rest, but recently Tashiro, by employing an exceedingly delicate test capable of detecting as little as 0.0001 milligram of CO_2, has shown that stimulating a nerve actually does increase CO_2 production by a slight amount. Another way of attacking the problem has been to ascertain whether or not the activity of the nerve causes an increase of temperature. If chemical changes are involved, one would expect such an increase to occur, as it demonstrably does in the contraction of muscle, but exceedingly delicate tests capable of detecting a rise of 0.000006 of a degree centigrade, have thus far failed to yield evidence of any temperature changes. On the assumption that the chemical processes involved are reversible, like the changes from the sol to the gel state and vice versa in colloids, we may understand the absence of the usual thermal indications of metabolic processes, since the heat liberated by one process would be quickly absorbed by the reverse one. Although excitation may not increase the temperature of a nerve, yet if the surrounding temperature is increased, the velocity of nerve transmission, like the velocity of chemical changes in general under these conditions, becomes more rapid. This increase of velocity has been adduced to support the chemical theory.

The problem of the nature of nervous transmission, like the problem of the cause of contraction, is one which has presented many difficulties, and has given rise to much experimental investigation. Although many points still remain obscure,

physiologists seem to be nearer its solution than they were a quarter of a century ago. Both problems doubtless involve many of the same elements, so that a solution of the one would go far toward elucidating the other. The recent advances in the study of the chemistry of colloids have afforded stimulating suggestions as to how both of the fundamental life processes of transmission and contractility may be interpreted in terms of the reversible changes of colloidal solutions. To the extent that these interpretations are successful, to that extent we may be said to succeed in explaining life.

It seems almost ridiculous to call blood a tissue, but it is often so designated because it contains living cells. The fluid part, or plasma, is a very complex mixture of dissolved proteins, fats, carbohydrates, salts, waste products of metabolism, and many other substances in smaller amounts. In the vertebrate animals the corpuscles, or cells of the blood, are of two kinds, the red and the white. The former are circular or oval cells, whose cytoplasm contains a large amount of a peculiar pigment called hemoglobin, which gives to the blood its red color. Hemoglobin is an iron-containing protein which takes in oxygen when this gas is relatively abundant in the lungs, and gives it up with great readiness where the oxygen pressure is relatively low, as it is in the tissues of the body. It is admirably adapted, therefore, to serve its function as an oxygen carrier to the tissues. In mammals the red blood cells have no clearly defined nucleus, although they originated in nucleated cells, but in most of the lower vertebrates the red cells are furnished with a distinct nucleus.

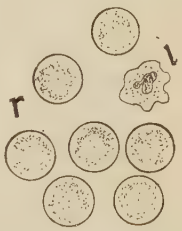

FIG. 21 — Human blood corpuscles: *r*, the red cells; *l*, a white cell.

The white blood cells, or leucocytes, are nucleated cells with naked protoplasm of irregular and changeable form. Their mode of behavior is closely similar to that of an Amœba, which will be described in a later chapter. We may think of our white corpuscles as really parts of us, but they appear to be little organisms quite as independent in their movements as if they

were parasites in our blood. They originate, however, from several organs of the body, particularly the lymph glands and the marrow of the bones. Unlike the red cells which are passively carried in the blood stream, the white cells have the power of active locomotion, and may even creep through the delicate walls of the capillaries and other thin membranes and pass out of the body entirely. Great numbers of them wander into the alimentary canal, and into the nasal cavity and mouth. These white cells engulf and devour materials of broken-down tissues, and they attack and destroy many kinds of bacteria which may have succeeded in invading the body. They are therefore important defenders of the organism, and they have the property of collecting in large numbers in regions of unnatural irritation and seats of infection to which they are attracted by some kind of chemical stimulus. In the colorless fluid called lymph there are many white cells, but no red ones.

In the blood of most animals below the vertebrates, there are, except in rare instances, no red cells. The corpuscles are usually of the colorless amœboid type, more or less like the leucocytes of our own body. Hemoglobin is present in the blood of many kinds of worms and molluscs, but it is generally dissolved freely in the plasma. In most of the molluscs and crustaceans there is a related oxygen-carrying compound called hemocyanin, which often gives the blood a bluish tinge, and which contains copper instead of iron.

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CHAPTER V

THE ONE-CELLED FORMS OF LIFE

A large proportion of the species of both plants and animals is composed of organisms consisting of a single cell. These forms are minute in size, and until less than three centuries ago, they remained completely hidden from the ken of man. The credit for revealing the existence of this world of minute life belongs, more than to any one else, to an industrious Dutch weaver and maker of lenses, Anton van Leeuwenhoek. Happening to examine some stagnant rain water, Leeuwenhoek saw to his surprise numerous small creatures swimming about in the most lively manner. These creatures were of the most diverse form and behavior, and Leeuwenhoek sent many accounts of his observations to the Royal Society of London, which published them in its *Philosophical Transactions*. Thus was started a series of discoveries which have opened up new fields of knowledge and have yielded practical results of inestimable value to the human race.

A few years after the cell theory was set forth by Schleiden and Schwann, it came to be recognized that microscopic organisms constitute a very motley lot, and that many forms are multicellular in composition, whereas others are composed of only a single cell. The one-celled animal organisms are called the Protozoa, and the one-celled plants, the Protophyta; but among these primitive forms of life the plant and animal kingdoms draw more closely together as if converging toward a common root. In fact, there are many organisms which so combine plant and animal characteristics that it is impossible to decide, except arbitrarily, to which group they should be assigned.

Taking up first the one-celled animals, we may find it advantageous to consider, as a representative of a large group of the

Protozoa, the common *Amœba proteus*. This well-known organism, which is a frequent inhabitant of ponds and streams, is often described as a minute, irregular, jellylike mass of protoplasm, containing a nucleus. There is no permanent cell wall, and the outer protoplasm, or ectoplasm, is more transparent and of somewhat firmer consistency than the inner, more fluid and granular endoplasm. The shape of an Amœba is subject to frequent changes due to the formation of lobes or projections called pseudopodia (literally false feet). When one watches a

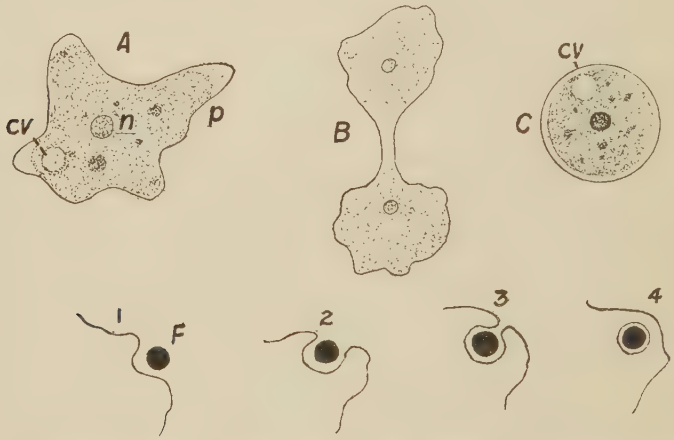

FIG. 22—*Amœba proteus: A*, active state; *B*, in division; *C*, in form of cyst. *cv*, contractile vacuole; *n*, nucleus; *p*, pseudopod showing clear ectoplasm at the tip; *1*, *2*, *3*, *4*, stages in the formation of a food cup and in ingesting a particle of food, *F*.

moving Amœba he may see, where a pseudopod is forming, that the ectoplasm appears to liquefy and then to give way, allowing the endoplasm to come to the surface. The latter then quickly forms a denser transparent layer where it comes in contact with the water. The granules of the protruding protoplasm are squeezed toward the center, thus causing the new pseudopod to become more transparent. Ectoplasm is formed at the expense of endoplasm and vice versa. The newly formed ectoplasm of a protruding pseudopod is adhesive, especially at the tip; this apparently forms a point of attachment to the solid surface on

which the Amœba creeps, and the contractility of the ectoplasm pulls the organism along. Then another pseudopod may be formed on the same side, and, by acting in a similar manner, enables the organism to creep farther in the same direction.

Amœboid movement has been explained in a variety of ways. One view is that it is caused by local variations in surface tension due to external and internal changes. Phenomena resembling amœboid movement can be brought about in oil drops suspended in water if one brings in contact with the surface of the drop some chemical which reduces the surface tension at the boundary between the water and the oil. The contraction of the surface on the other sides of the drop causes the oil to protrude at the weakest point much like a pseudopod. By using the proper kinds and strengths of material very close imitations of the movements of an Amœba can be produced, but there are important differences presented by the behavior of a real Amœba which it is difficult to interpret according to the surface tension theory. In a living Amœba pseudopodia may be bent back and forth, thus showing that they possess some degree of rigidity; and when they are being withdrawn into the body, the outer layer often becomes wrinkled, which we should not expect it to do if its surface tension were the cause of the withdrawal. It is probable that the seat of contractility is not limited to the merest surface film of the ectoplasm; the whole ectoplasm apparently contracts much like muscular tissue. The protoplasm of an Amœba when it passes from the sol to the gel state becomes more contractile, and it is probable that the changes in the viscosity of the outer protoplasm play an important part in the movements of the organism.

Amœba, like numerous other primitive organisms, manages to perform its several functions without the aid of specialized organs. The exchange of substances involved in respiration is carried on through the entire surface of the body. Circulation is adequately provided for by the irregular movements of the fluid endoplasm. Excretion doubtless occurs through the exterior surface, but there is a small organ called the contractile vacuole also concerned with this function. This vacuole as it becomes

filled by the fluid which drains into it from the surrounding protoplasm discharges its contents to the outside and then proceeds to fill up anew. This periodic filling and discharge results in washing the protoplasm free from its soluble products of excretion. The quantity of water passing through an Amœba in the course of twenty-four hours is several times the bulk of the organism. If a corresponding internal lustration occurred in a man he would have to drink several barrels of water a day.

Amœba resembles higher organisms in responding to stimuli by active movements. A prick of a needle, or the application of an injurious chemical to one side, causes the organism to creep away from the stimulus. Amœba travels away from a source of light, but it is attracted by many chemical substances, especially those whose presence indicates food. The process by which food is taken into an Amœba is not so simple as the older descriptions would lead one to infer. Amœba was supposed simply to flow around a morsel of food and take it in much as a drop of water may draw in a minute splinter of glass which is brought against it. The so-called artificial Amœbas previously mentioned may be caused to engulf particles to which they adhere, the objects being drawn in by the tension of the surface film. The observations of Schaeffer, Kepner, and Taliaferro have shown that food-taking in Amœba involves definite responses to stimuli derived from the food in advance of actual contact. As Amœba draws close to food, pseudopods are thrust out on either side of the object, forming what is called a food cup. The projections finally surround the object completely, after which it is drawn into the endoplasm. There it becomes inclosed in a space, the food vacuole, which is a sort of improvised stomach where digestion takes place as a result of the secretion from the endoplasm of a fluid containing digestive ferments. After the absorption of the soluble products of digestion, the residue that may remain is passed, apparently through any part of the ectoplasm, to the outside.

Amœba feeds upon all sorts of minute forms of plant and animal life. Jennings has described how an Amœba followed a round

cyst of a Euglena which rolled ahead of its pseudopods, the pursuer frequently changing the direction of its course as the cyst rolled to this side or that. After about fifteen minutes when the cyst was about to be stopped by an obstacle, a passing infusorian whisked the ball out of the way of its pursuer. Amœba does not confine its attacks to organisms smaller than itself. It may tackle a relatively large infusorian, or a multicellular animal, such as a rotifer, or small worm. Mast and Root have described an Amœba which had seized a much larger Paramœcium in its food cup. As the food cup could not engulf the entire body of the Paramœcium, it pinched the prey in two and swallowed the part which was seized. Sometimes Amœbas take in long threads of algæ which become coiled up in the endoplasm as they are pulled into the body (Fig. 24).

FIG. 23—Amœba following an encysted Euglena, the figures representing the successive stages in the pursuit. (After Jennings.)

The pursuit of food at a distance involves a very delicate sensitivity which is all the more remarkable in an organism which has no trace of sense organs or nervous system. Schæffer has shown that Amœba can sense at a distance even inert objects, such as clean particles of glass or carbon. It is scarcely probable that these substances exercise any chemical attraction; they may possibly affect the sensitive ectoplasm through the slight resistance of the water about them as they are approached. They may be sensed, therefore, somewhat as a blinded bat senses the objects in a room which he avoids in the course of his flight. But in whatever way they are detected, the extreme delicacy of responsiveness which Amœba exhibits is not often equalled by that of the highest animals.

Under unfavorable conditions such as those produced by the drying up of a pond, or the development of injurious products of decay in the water in which it lives, Amœba may assume a spherical form and secrete about itself a protective wall, or cyst. In this state Amœba may tide over bad times until more favorable conditions recur, when it breaks out of its cyst and resumes an active life. In the encysted state some kinds of Amœba may resist desiccation for at least several months. If we gather up a bit of dust almost anywhere, say from the top of our writing table, and place it in a solution of thoroughly sterilized food material, we shall probably find in the bacterial scum that makes its appearance in a few days, a number of Amœbas. Within their cysts some Amœbas may resist several hours of boiling. The toughness and resistance of these animals stand in a rather striking contrast to the delicacy of their responses when in the active state.

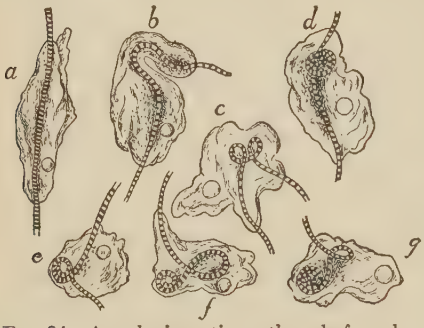

FIG. 24—Amœba ingesting a thread of an alga, Oscillaria; *a-g* represent successive stages in taking in and coiling up the thread. (After Rhumbler.)

The common Amœba multiplies by process of binary fission in which the nucleus divides by a process of mitosis accompanied by the elongation and constriction of the cytoplasm by which finally the organism is cut into two daughter Amœbas. These soon grow to the usual size, and then division may take place again, the process repeating itself, so far as we know, as long as conditions are favorable. At times, a modification of this process occurs during the process of encystment, when there may be repeated divisions resulting in the production of a large number of very small amœboid organisms known as spores. These ultimately break out of the cyst and grow into ordinary Amœbas.

When we consider all these activities of Amœba from the standpoint of adaptation it becomes apparent that the life of this

organism consists of a series of reactions which tend to preserve the integrity of the individual. The organism creeps away from injurious agencies; it reacts positively to weak stimulations which may mean food, and to light contact which may mean food or a substratum upon which to crawl. Under unfavorable conditions it protects itself by a very resistant cyst, and it secures the perpetuation of its race by dividing by fission. Amœba, even with its very limited equipment, solves its problems of getting on in the world in very much the same way as a higher animal does. Whether it possesses conscious awareness is a question about which psychologists may differ. As Dr. Jennings remarks in comparing the behavior of Amœba with that of a dog: "If Amœba were so large as to come within our everyday ken, I believe it beyond question that we should find similar attribution to it of certain states of consciousness, a practical assistance in foreseeing and controlling its behavior. Amœba is a beast of prey, and gives the impression of being controlled by the same elemental impulses as higher beasts of prey. If it were as large as a whale, it is quite conceivable that occasions might arise when the attribution to it of the elemental states of consciousness might save the unsophisticated human being from the destruction that would result from the lack of such attribution."

The common Amœba has enlisted the interest of many of the foremost biologists, who have endeavored to ascertain how far the behavior of this simple creature can be explained as the result of the known processes of the physical world. The more intimate our acquaintance with the ways of this animal has become, the more complex and varied its behavior has been found to be. Some of the simple physical explanations of its movements have been shown to be inadequate. This does not prove that a mechanistic explanation of its behavior is ruled out. In fact, further knowledge of the properties of colloids affords a very plausible interpretation of some of the peculiarities of amœboid movement. Even the simplest activities of living beings present difficult problems from the standpoint of the physicist and chemist. We have been prone, however, to overestimate the

simplicity of Amœba. It is indeed remarkable that with its relatively undifferentiated and ever-changing protoplasm it is able to get through the world at all, but it should be borne in mind that Amœbas have been on our planet for many millions of years, and that each Amœba living today has the experience of all these ages behind it. If all life sprang originally from a single source, all kinds of organisms are in one sense equally old. Some, like ourselves, have gone on and become highly developed creatures, but others have remained near the foot of the tree of life and have perfected themselves for living in their humble sphere. And they have succeeded in doing this surprisingly well.

The common Amœba (*A. proteus*) is but one species of a very large group of closely related forms, occurring both in fresh waters and in the sea. Then there are the soil Amœbæ, which make their living by devouring bacteria and other kinds of organic food in the soil. They thus indirectly influence soil fertility, and are therefore coming to be studied seriously by the scientific agriculturalist. There are several Amœbæ which are parasitic. Amœbic dysentery, which is prevalent in many parts of the world, is caused by Amœbæ which burrow into the walls of the intestine and often cause most distressing symptoms. *Endamœba gingivalis* occurs in the mouth and in decaying teeth; and other Amœbæ are found in other parts of the body. From the standpoint of the pathologist, the Amœbæ are coming to assume a position of considerable prominence.

Fig. 25—Shells of Foraminifera from the bottom of the Indian Ocean.

Many of the more remote allies of the Amœbæ secrete a shell which partially incloses the body. The shells of the marine group Foraminifera build up, by their accumulation at the sea

bottom, the chalky deposits which are found in several parts of the ocean. Our common chalk is composed mainly of the remains of these small shells. Another extensive marine group, the Radiolaria, consisting of several thousand species, form supporting skeletons, commonly of silica, which are remarkable for the beauty of their radially symmetrical structure. The Foraminifera and the Radiolaria live upon the smaller organisms which they catch with their fine pseudopodia, and they serve in turn as food for higher animals.

Fig. 26—Skeletons of Radiolarians. (After Haeckel.)

The group of protozoans known as the Infusoria are very different in appearance and mode of life from the forms we have been considering. They possess a well defined contour with a permanently differentiated ectoplasm, generally furnished with cilia, which serve as organs of locomotion and frequently also as means of securing food. A typical representative of the Infusoria is the common Paramœcium, which is a familiar object to every one who has taken a laboratory course in biology. This organism owes its popularity to the fact that it can be obtained in abundance by making an infusion of hay, or other vegetable material, in water from some pond or stream. After a few days, when the bacteria become abundant, the Paramœcia multiply rapidly and are soon found in large numbers. The elongated body of Paramœcium is uniformly covered with short cilia whose oblique beating causes the organism to swim through the water in a spiral path. There is a broad, oblique depression on one side of the body, leading posteriorly to a narrow gullet, which terminates in a small enlargement called the crop. The bacteria and other fine particles which serve as food are swept down the gullet by

ciliary currents and collect in the crop, where at intervals the contents become pinched off by a contraction of the surrounding protoplasm. In this way a mass of food material, together with a small amount of water, is forced into the body, forming a food vacuole. The food vacuoles are carried about by a slow current

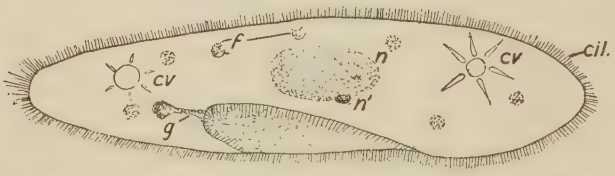

FIG. 27—*Paramœcium caudatum: cil*, cilia; *cv*, contractile vacuoles; *f*, food vacuoles; *g*, gullet with crop at end; *n*, macronucleus with the micronucleus, *n'*, beside it.

of the semi-fluid endoplasm, and their contents become digested and absorbed during their course. The undigested residue is forced out of the body through a region of the ectoplasm lying behind the mouth. There are two contractile vacuoles which function much as in Amœba.

FIG. 28—*Paramœcium aurelia* dividing. The macronucleus, *m*, and the two micronuclei, *nk*, *nk'*, are in division; *o*, *o'*, mouth.

Paramœcium, like the Infusoria in general, has two kinds of nuclei. Near the middle of the body is the large oval nucleus, called the meganucleus, with a much smaller micronucleus lying close beside it. During fission—for Paramœcium reproduces exclusively by fission—both these nuclei elongate, become constricted in the middle, and divide, the nuclear division being followed by a transverse fission of the whole body. The meganucleus divides amitotically, while the micronucleus undergoes a modified process of mitosis, breaking up into a large number of chromatin threads, or chromosomes, which become pulled apart toward the two poles. Divisions may occur in Paramœcium as frequently as once in twenty-four hours, and they may be continued for a great many generations—perhaps indefinitely. At times, however, fission is inter-

rupted by a form of sexual reproduction, or conjugation. Individuals become attached by their oral surfaces and swim about in pairs. In the meantime, changes take place in the nuclei, which will be described in a later chapter. Each individual receives nuclear material from the other, and after this exchange the organisms separate and then undergo a further series of divisions.

The Infusoria constitute a large group, represented by both marine and fresh-water forms, and also by parasites within the bodies of higher animals. Some of the Infusoria attain a high degree of structural organization which rivals in complexity that of many of the multicellular animals ranking much higher in the scale of life.

The Protozoa belonging to the group of Flagellata, or Mastigophora, are characterized by the possession of flagella, or threadlike organs resembling a whip lash. The flagella are usually one or two, rarely more, in number, and it is by the movements of these organs that the flagellates swim through the water. The group of flagellate organisms is a sort of synthetic group, containing representatives of both plant and animal kingdoms. We may consider these primitive forms as a sort of basic group, from which both the higher plants and the higher animals took their origin.

Of the plantlike flagellates, one of the best known is the common *Hæmatococcus*, or *Spherella pluvialis*, whose presence gives sometimes a greenish and sometimes a reddish color to the puddles of water in which it often occurs. In the active condition, Hæmatococcus is oval in shape with a central mass of protoplasm separated from the outer cellulose wall by a space, which is crossed by several transparent protoplasmic strands. At one end there is a protoplasmic eminence, which gives rise to a pair of flagella that protrude through the cell wall. Near the base of these flagella is a reddish body, called an eye-spot, which is supposed to be sensitive to light. There is a round nucleus near the center, and the cytoplasm is colored green by chlorophyll, or red by hæmatochrome, which is only a modifica-

tion of chlorophyll. Within the cytoplasm are several plastids which are concerned with the formation of starch.

Hæmatococcus is able to utilize as food only those substances which can diffuse through its cellulose wall. It employs the same mineral substances that are used by the higher plants, and it is similarly dependent upon sunlight, with the aid of its chlorophyll, for building up these materials into living tissue. Its method of nutrition is holophytic, or plantlike, in contrast with that of Amœba, which is called holozoic. In its ordinary method of reproduction, Hæmatococcus divides within its cell wall into two, and then into four, smaller individuals, which break out

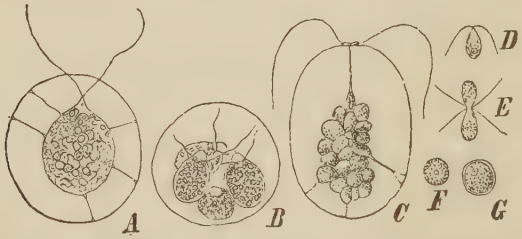

FIG. 29—*Hæmatococcus* (*Sphærella*) *pluvialis: A*, free-swimming stage; *B*, division within the cell to form four smaller individuals; *C*, *Hæmatococcus bütschlii* forming small gametes; *D*, a free motile spore; *E*, the conjugation of two gametes; *F*, *G*, zygotes formed as the result of conjugation. (After Blochmann.)

of the old encasement and lead a free-swimming life. At intervals, several divisions may rapidly succeed one another within the old cell wall, and give rise to thirty-two or sixty-four small flagellated spores, which leave the old cyst through a rupture in its wall. These small spores are supposed to meet and fuse together, the nuclei combining as well as the cytoplasm. This process of conjugation, or sexual reproduction, is followed by a period of growth and encystment, in which the flagella disappear and the whole organism assumes a spherical form. Encystment also occurs without conjugation. In the encysted state the organism may resist prolonged drought. One may keep the dried cysts for a long time and obtain new active forms at will by placing the cysts in rain water exposed to sunlight.

On account of its green coloring matter, cellulose wall, and

mode of nutrition, Hæmatococcus is considered to be a typical plant. Many other flagellates are quite devoid of chlorophyll and take in solid food. These forms are typical animals. Many flagellates live upon decaying organic substances, which they imbibe through the cell wall. Such forms are called saprophytes. Their mode of nutrition is similar to that of the higher fungi, which are undoubtedly plants, although they have no chlorophyll.

FIG. 30—*Euglena viridis*, a flagellate which combines plant and animal characteristics: *cv*, contractile vacuoles; *e*, eye spot; *m*, mouth; *n*, nucleus.

A considerable number of flagellates are unfortunately parasites. Among the most important of these are the trypanosomes, which infest the blood of vertebrate animals, causing in some cases severe diseases, such as surra and dourine in horses. One species of this group, *Trypanosoma gambiense*, is responsible for the sleeping sickness which is widespread among the natives of Africa. This disease, as its name implies, is characterized by symptoms of extreme drowsiness in its later stages, and it is almost uniformly fatal. It is estimated that in the Uganda district alone, it carried off 100,000 natives in four years. The fact has been established that the sleeping sickness may be conveyed by the bites of the tsetse fly, but it has not been found feasible to exterminate this insect, and as treatment for the disease has not been thoroughly applied, little has been done to check the woeful slaughter of black humanity that has gone on in Africa for so many years.

FIG. 31—Trypanosomes.

One of the noteworthy traits of the flagellates is their tendency to form colonies. The individuals which are produced by fission may remain together, instead of separating in the usual manner, and thus build up colonies which assume a variety of forms. Sometimes they consist

of linear aggregates, sometimes there are branching colonies, or again the organisms may constitute a flat plate, as is the case in Gonium which consists of sixteen cells imbedded in a gelatinous matrix. In Pandorina and Eudorina we have a spherical colony of sixteen to thirty-two cells, each of which is furnished with a pair of flagella at its outer end. The highest stage in colony formation is found in the spherical form Volvox, which may consist of several thousand individual cells.

In the class of Protozoa known as the Sporozoa, reproduction, as the name suggests, occurs by the formation of spores. The Sporozoa are a parasitic group, all the species obtaining their living by making themselves a nuisance to other organisms. Their victims include all sorts of animals from man to the Protozoa themselves, and there are even sporozoan parasites of sporozoan parasites. The species are numbered by the thousand. A follower of Paley might derive some consolation from the fact that in many cases they appear to cause little harm, but, on the other hand, they are responsible for some of the most injurious and fatal maladies that afflict the animal creation. Most of the Sporozoa live for at least a part of their life within the cells of their host. A great many species attack the epithelial cells of the alimentary tract, especially in the invertebrates. A severe disease of silkworms, known as *pébrine*, which at one time almost destroyed the silk industry of France, is known to be caused by a minute Sporozoön. Owing to the laborious investigations of Louis Pasteur, who traced the cause of the malady and ascertained the mode of its transmission, methods were perfected by which the silkworms could be kept free from this fatal and highly contagious disease. Thus the silk industry, not only of France but of several other countries, was saved from impending ruin.

One group of the Sporozoa, the Hæmosporidia, are parasites within the red blood cells of vertebrate animals. The disease of cattle known as Texas fever is caused by a small hæmosporidian, which may be conveyed from one animal to another by the bites of wood ticks. The most important sporozoan disease, at least from our human point of view, is malaria. There are few

achievements of medical science which have proved of greater importance to man than the discovery that malaria is caused by a sporozoan parasite, which passes through a part of its life history in human blood, and the other part in the body of the mosquito. It has been repeatedly and conclusively shown that the only way in which a person can normally contract malaria is by being bitten by a mosquito of the genus Anopheles or of some other related genus. It is in this way that the parasites gain entrance to the blood. Then they penetrate the red blood corpuscles and ultimately destroy them. The parasites multiply by spore formation and continue to attack new corpuscles until the disease reaches its height. They may finally die off and allow the patient to recover, or they may linger indefinitely, giving rise to a chronic malarial condition.

The whole increase of malarial parasites in the blood is brought about by asexual multiplication, the peculiar environment afforded by the mosquito's body being requisite for the completion of the sexual cycle. The early stages in the formation of both male and female gametes, however, take place in human blood. When the blood is sucked into the stomach of the mosquito, those parasites which were beginning to differentiate into sexual cells rapidly complete their development. The female gamete is much like an ordinary, fully developed parasite, but the cells forming the male gamete put out long, filamentous projections, which ultimately become free and active. These meet and fuse with the female gametes, which then become more or less motile, and work their way through the epithelial lining of the mosquito's stomach and grow into cysts just beneath its outer wall. An examination of the stomach of a mosquito several days after it has bitten a malarial patient, shows the wall of the stomach to be studded with a number of rounded cysts. Unfortunately these do not make the mosquito sufficiently ill to keep her from attacking human beings and spreading the disease.

Within these growing cysts there is a rapid development of spores, which, when mature, take on a fusiform shape. These break out of the cysts and wander through the tissues of the

host, many of them lodging in the salivary glands, from which they gain access to human beings when the mosquito takes her

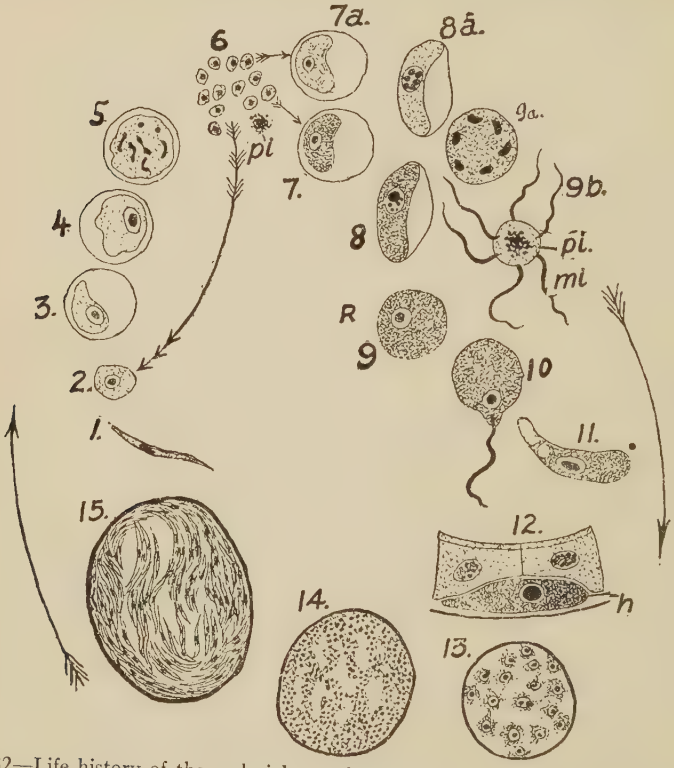

FIG. 32—Life history of the malarial parasite Plasmodium: *1*, sickle-shaped sporozoite as it enters the blood through the bite of a mosquito; *2*, amœboid form assumed by the parasite when it enters a red blood corpuscle; *2–5*, stages in the growth of the parasite within the red corpuscle; *6*, the amœboid bodies formed by the division of the parasite; these enter new corpuscles and repeat the cycle as indicated by the arrow; *7–15*, the sexual cycle in the mosquito; *7–9*, female gametes; *7a–9b*, formation of male gametes; *10*, union of male and female gametes forming the zygote, *11; 12*, zygote which has penetrated the wall of the stomach of the mosquito; *13–15*, growth of this cell and the multiplication of its nuclei and the formation of the spindle-shaped bodies, *15*, which break out of the cyst and wander through the body of the mosquito; some of these lodge in the salivary gland, whence they may enter human blood and start a new cycle. (After Schaudinn.)

fill of blood. Then the asexual cycle starts again in the new human host, producing its chills and fever and all the other symptoms of this disagreeable malady.

When we turn to the study of the unicellular plants, or Protophyta, we encounter an almost endless wealth of different types. Some of the forms described under the group of flagellates are really plants. In a good many of the one-celled green algæ, such as the Protococcus, which often grows on tree trunks or stones in damp places, there are no flagella in the adult state, but the spores are provided with a pair of them, much as in Hæmatococcus. In the large group of diatoms, the protoplasm is inclosed between a pair of siliceous and often beautifully sculptured valves which fit closely together, like a pill box and its cover. These diatoms, which are often exceedingly abundant in both fresh and salt waters, afford an important food supply for higher animals, and their shells form the diatomaceous earth which occurs abundantly in certain deposits. Allied to the diatoms are the beautiful green desmids, which are the delight of the amateur microscopist. There are numerous one-celled blue-green algæ (Cyanophyceæ), whose peculiar color is due to a pigment called phycocyanin, a compound allied to chlorophyll. These forms have no clearly defined nuclei, although the chromatin in some species shows a tendency to aggregate into a central body and to behave in division in a way that is suggestive of mitosis in higher forms. In many of the primitive green algæ, the cells may be united into long rows, or filaments. In fact, among the primitive plants there are gradations into multicellular types in a number of the different classes.

A group of much importance are the yeasts, whose practical value arises from the fact that they are the agents which effect the fermentation of bread, beer, wine, and many other common articles of human consumption. Multiplication regularly occurs by the formation of buds, which become constricted off from the parent cell. Sometimes a process of sporulation occurs, when the contents of the cell divides twice to form four spores. There are many kinds of yeasts, each responsible for its own peculiar type of fermentation, but there are also many kinds of fermentation

FIG. 33—Cells of yeast showing budding and in one case four spores.

which are due to other micro-organisms, especially the bacteria.

The real relation of the yeast to fermentation, although suspected by several observers since the prevalence of these organisms was noted in fermenting materials, was first clearly established by Louis Pasteur. It was commonly held that fermentations were set up spontaneously, or by the addition of a small amount of albuminous matter, which was supposed to impart a sort of molecular movement that broke down the fermenting material into simpler constituents. In a series of carefully controlled experiments, Pasteur showed that ordinary fermentations do not occur in the absence of micro-organisms, and that different kinds of organisms often produce very different chemical changes. Ordinary alcoholic fermentation is caused by yeasts. Lactic acid fermentation, which takes place in the souring of milk, was shown by Pasteur to be caused by a small kind of bacterium. Butyric acid fermentation he found to be caused by other organisms. Mixed fermentations sometimes occur, and these were shown to be caused by a mixture of different organisms, whereas in pure fermentation, there was only one kind of organism that prevailed. The work of Pasteur on fermentation brought order out of what had hitherto been a state of chaos and confusion. Knowing what caused the different kinds of fermentation, scientists were able to bring them under control, and this knowledge was soon put to practical use. Beers and wines at that time suffered from certain diseases; the fermentations by which they

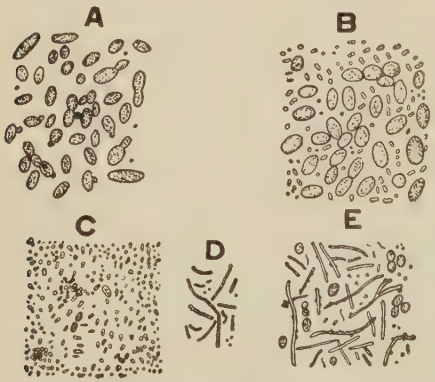

FIG. 34—Organisms found in diseased wines: *A*, yeast cells of normal vinous fermentation; *B*, acid wine in early stages of deterioration; *C*, a later stage of the same malady; *D*, ropy wine; *E*, bitter wine. (From Holmes's *Louis Pasteur*.)

were produced went wrong for some reason, and greatly deteriorated the product. Pasteur traced the cause to foreign micro-organisms which produced undesirable kinds of fermentation. By carefully selecting the kinds of yeasts used in brewing beer and in fermenting wine, it was shown that these diseases could be avoided, and by heating beers and wines it was found that their subsequent deterioration through living ferments might be effectually prevented. Once the cause of the trouble was located, the remedy, as in so many other cases, was not difficult to apply.

The most primitive, and also the most extensive, group of the Protophyta are the bacteria. They are very minute, some being visible only with the highest powers of the microscope. But beyond the limits of vision, there are many forms of life whose existence is indicated by the effects produced by their activity. These are the so-called filterable viruses, which are able to pass through very fine filters. There are several diseases which are now known to be caused by these invisible organisms.

Bacteria have no clearly defined nucleus and show little differentiation of structure. There is an outer cell wall and frequently a more or less gelatinous capsule. Some forms are provided with one or more flagella, which are employed in locomotion. Bacteria are usually rod-shaped (Bacilli), spherical (the Cocci), or spiral (the Spirilli and Spirochætes). Their usual mode of multiplication is by simple fission. Some species, such as the hay bacillus and the bacilli of tetanus and anthrax, form spores, which are relatively resistant to destructive forces. The food requirements vary greatly with different species; a great many are saprophytic, subsisting on the products of decaying plants or animals. There are numerous parasitic forms which require

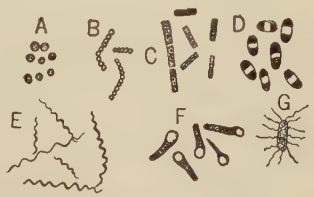

FIG. 35—Forms of bacteria: *A*, Staphylococci; *B*, Streptococci; *C*, bacilli of anthrax; *D*, bacilli of the plague; *E*, *Spirochæta pallida*, the germ of syphilis; *F*, tetanus bacilli showing spores in one end; *G*, the typhoid bacillus.

the material supplied by their living host.[1] A few species build up their protoplasm from purely mineral compounds. One of the sulphur bacteria, for instance, thrives on a diet made up as follows:

Ammonium sulphate	1 gram
Potassium phosphate	1 gram
Magnesium carbonate	1 gram
Water	1 liter

The bacteria have no chlorophyll, as the green plants have, to aid them in making living protoplasm out of a few simple mineral salts. How do they bring about the change?

Bacteria occur in all sorts of situations—in the sea, fresh water, the soil, and in the bodies of plants and animals. As a consequence of their abundance and wide distribution, they play an important part in the general economy of organic nature. The chief agents of putrefaction and decay, they perform the very valuable service of resolving the dead bodies of organisms into the constituents of the soil, whence they again become available as food for plant life. The final products of the decomposition of proteins are carbon dioxide, water, and ammonia. The higher plants commonly take in their nitrogen in the form of nitrates, and the conversion of ammonia and its salts into a form available for plant food is effected by a group of bacteria called nitrifying bacteria. Some of these, through a process of oxidation, convert ammonia and its salts into nitrites, or salts of nitrous acid (HNO_2). Other bacteria cannot act on ammonia directly, but convert the nitrites into nitrates, or salts of nitric acid (HNO_3). There are still other forms, the nitrogen-fixing bacteria, which are able to fix, or combine, the free nitrogen of the air and convert it into compounds which can be used as food by higher plants. Some of the latter bacteria live freely in the soil, but others live within tubercles on the roots of leguminous plants, such as clover, beans, and peas. Hence crops of these plants are grown to supply nitrogen to the soil.

[1] The tubercle bacillus and some other parasitic bacteria may live upon purely inorganic constituents.

Much attention is now devoted to the bacteriology of water, dairy bacteriology, the bacteriology of sewage, the applications of bacteriology to various industries, to say nothing of the bacteriology of plant and animal diseases. With courses in the subject in universities and colleges of medicine, and researches carried on by government bureaus, institutes of medical research, and agricultural experiment stations, bacteriology has come to rank as one of the most important branches of biological science. Most of this remarkable development is the product of the last fifty years. The young science shows no sign of slackened growth, and is doubtless destined to undergo further remarkable developments in the decades to come.

A most important chapter in the history of bacteriology was furnished by the controversy over the spontaneous generation of life. Formerly even so highly developed animals as mice, frogs, insects, and worms, were supposed to originate spontaneously out of mud, slime, or decaying matter. The Dutch physicist, Van Helmont (1577–1644), gives a recipe for obtaining mice, which consists in putting some grains of wheat in a container, along with some old dirty linen. After a few days the mice will make their appearance. About the first to attack the problem experimentally was the Italian physician, Francesco Redi (1626–94). Observing the presence of blowflies about decaying meat, Redi conjectured that possibly the flies might have something to do with the presence of maggots, which were at that time supposed to originate in decaying animal matter. He tried the simple experiment—people were not much given to experimentation in those days—of keeping meat protected from flies by a screen of gauze. In meat so protected no maggots made their appearance. Moreover, Redi found that the flies often laid eggs upon the screen, and he proved that these eggs produced the maggots which later transformed into flies. These and other experiments overthrew the grosser forms of the doctrine of spontaneous generation, but when more came to be known about the life of micro-organisms and their occurrence in fermenting and putrefying materials, the old question presented itself anew.

The Irish priest Needham subjected infusions of vegetable matter to boiling in glass flasks which were subsequently closed with a cork, and he concluded that the micro-organisms which made their appearance in the infusions in the course of a few days must have been spontaneously produced. The sagacious Abbé Spallanzani, however, suspecting that the germs of micro-organisms might have gained access to Needham's flasks from the air, boiled infusions in a glass vessel with a narrow neck, which was sealed in a flame while the contents of the flask were still hot. The infusions, thus completely protected from the outside air, were found to keep clear and free from minute forms of life for a long time.

Later investigators, however, in repeating the same experiment, obtained a different result. The French naturalist Pouchet, in his large work entitled *Hétérogénie*, reported numerous experiments in which living forms developed in nutrient solutions which had been thoroughly boiled and which had been adequately protected against the entrance of possible germs from the outside. It was concluded therefore that life must have been developed spontaneously from the non-living organic substances of the infusions.

These experiments were followed with keen interest by Pasteur, whose work on fermentation, to which we have alluded, led him to believe that specific fermentations were caused by particular species of micro-organisms. Pasteur was naturally disposed, therefore, to be skeptical in regard to the spontaneous origin of life from non-living matter. Suspecting flaws in the experimental procedure of Pouchet, he began to investigate the problem by a series of very carefully conducted experiments. He found that life failed to develop in sealed flasks whose contents had been sufficiently boiled. He found that air in different localities had very different powers of generating life when admitted to flasks containing boiled infusions. The air of a city street or a field almost invariably caused putrescence, while the pure mountain air of the Alps rarely caused any contamination. It was not the air, he argued, but something in the air which caused life to

develop. This something, he found, could be excluded by supplying infusions with air passed through a cotton filter, or allowed simply to bubble slowly through water. In one experiment, which is particularly instructive, Pasteur boiled an infusion in a flask with a long, curved neck. The contents were found to remain pure, because, according to Pasteur, the germs floating in the air were caught by the sides of the long tube as the air enters the flask. If, however, the liquid was tilted, so that some

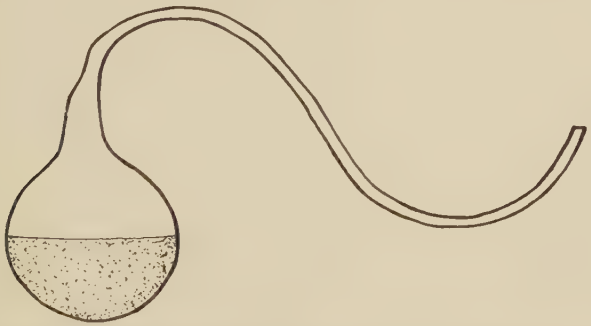

FIG. 36—Flask with long, curved neck used by Pasteur in experiments on spontaneous generation.

of it could run into the tube, it was found that turbidity and putrefaction soon appeared in the infusion.

In these investigations many puzzling difficulties were encountered, owing, as was later shown, to the circumstance that some kinds of bacteria when in the form of spores can be boiled and nevertheless subsequently grow and multiply. Heating to a temperature of 120° C., which is possible under a sufficient amount of pressure, was found to kill all forms of life. Through a long series of ingenious and carefully controlled experiments, for the field presents many pitfalls, Pasteur and his co-workers finally succeeded in showing, to the satisfaction of the scientific world, that where substances are first thoroughly sterilized and kept free from all chance of contact with germs from the outside, they do not engender living organisms. So far as our knowledge goes, the dictum *Omne vivum e vivo*—all life from antecedent life—represents a general truth. Moreover, as these experiments

also showed, all life comes from antecedent life of the same kind—a fact of far-reaching importance in elucidating the phenomena of fermentation and disease.

How the gap between the inorganic and the organic world was originally crossed remains an unsolved problem. The study of microscopic organisms, with the greatly improved methods of modern technique, has revealed complexities of structure which were unsuspected by the older observers. To suppose that such forms as Infusoria, for instance, arose spontaneously out of lifeless compounds, is much like supposing that a house should suddenly build itself out of a pile of bricks. It is not improbable that the exceedingly minute forms known as the filterable viruses are much more simple than any of the organisms with whose structure we are acquainted. But there is a wide difference between the simplest imaginable living creature and the most complex compound that can be fabricated by the chemist. Beginning with the synthesis of urea out of inorganic constituents by Wöhler, in 1828, organic chemists have built up one organic compound after another, going on, step by step, from the simple to the complex, until many of the carbohydrates and some of the simple proteins are now artificially synthesized in the laboratory. Whether chemists will ever succeed in fabricating living protoplasm it would be unsafe to predict. If they do, it would seem probable that the same transformation has been effected in nature, perhaps many times. A few scientists, Helmholtz, Lord Kelvin, and more recently, Arrhenius, have suggested that minute forms of life may have been wafted to the earth from other parts of the universe. More or less foreign matter rains down upon our planet from somewhere in interstellar space, and if some of it came from other worlds that support life, it is of course possible that very primitive organisms might have been carried by this means to our earth. This theory, however, only puts the solution of the problem back a little, although it is possible to maintain, as Ritter has done, that life might never have originated at all, but has been traveling about the universe from pillar to post throughout all eternity.

I do not see how this hypothesis can be definitely disproven, although this is not necessarily saying much in its favor. A more widely accepted view among biologists is that living matter is the product of a slow evolution from inorganic materials. There have been several hypotheses as to how the transition might conceivably have been made, but the subject is still in a highly speculative stage. It may long remain so before the problem is finally settled, or the next few years may bring discoveries that place it in an unexpected light.

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CHAPTER VI

MICRO-ORGANISMS AND DISEASE

The study of the one-celled forms of plant and animal life has led to one of the greatest achievements in the history of science—the discovery of the causes of contagious and infectious diseases. For ages the reason for the spread of infections and epidemics remained a complete mystery. Among primitive peoples in general, disease is interpreted as due to the activities of spirits which invade the body of the afflicted person. If these spirits are of evil intent they may make all sorts of trouble, and there is no relief until they take their departure. In accordance with this theory, which is a natural corollary of the belief in animism that prevails so widely among uncivilized peoples, the treatment of disease consists in supplications, threats, incantations, magic rites, and various other devices by which the intruding spirits may be induced or forced to leave the body of their victim. In the state of knowledge that obtains among primitive men, the doctrine of animism is a perfectly reasonable theory, and the practices based upon it follow quite naturally. Even the literature of civilized peoples is full of indications of the belief in demoniacal possession, a Church of England baptismal formula of the time of Edward VI containing the words "I command thee, unclean spirit, in the name of the Father, the Son, and of the Holy Ghost, that thou come out and depart from these infants."

But amid the well-nigh universal prevalence of the doctrine of demoniacal possession, we find back in the period of greatest development of Greek thought, in the fifth century before Christ, the beginnings of a scientific theory of medical treatment. The great Hippocrates, deservedly known as the founder of medicine, taught that disease is the result of natural causes and should be

treated by natural means. In the succeeding centuries the healing art came to fall more and more within the province of science. Efforts were made to discover what produces abnormal conditions in the body, but the problem of the transfer of disease baffled all attempts at solution. In an epidemic which spreads over a population there is apparently something which passes from one person to another which causes the malady to develop. By some it was thought to be "morbid matter"; by others a kind of movement analogous to a vibration, but none of the theories really threw any light upon the mysterious phenomenon. Until nearly the last quarter of the nineteenth century, the cause of contagion was as much of an enigma as it was in the days of Hippocrates.

The so-called germ theory of disease had been entertained more or less seriously ever since the first discovery of minute forms of organic life, but it remained for a long time a mere plausible conjecture, unsupported by experimental evidence. Pasteur's work on fermentation and spontaneous generation, and his successful attack upon the diseases of wine and beer, naturally disposed him, as it did several of his contemporaries, to look with favor upon the doctrine that infectious diseases might result from the presence of micro-organisms. In the course of his work he had often reflected upon the prophetic remark, made over two hundred years before, by the English chemist, Robert Boyle, that "he that thoroughly understands the nature of ferments and fermentation shall probably be much better able than he that ignores them to give a fair account of the diverse phenomena of several diseases." Pasteur's studies on the diseases of silkworms, which resulted in connecting these maladies with the presence of specific micro-organisms, served to give further support to the germ theory. In Scotland the celebrated physiologist, Joseph Lister, who had followed Pasteur's work on fermentation and spontaneous generation with the keenest interest, came to the conclusion that the cause of infections, which in those days so frequently resulted from surgical operations, was to be sought in micro-organisms which gained access to the

wounds from the hands and instruments of the operator, or from the floating matter of the air. Accordingly Lister insisted on having everything connected with a surgical operation thoroughly sterilized. The hands of the surgeon, the instruments, and the bandages employed were washed in a solution of carbolic acid, and dressings, sterilized in the same solution, were applied to the wound. As a result of these precautions, the mortality from operations was reduced to a surprising extent. Previously, wounds almost always became charged with pus, and very commonly developed gangrene and were followed by general blood poisoning. Hospitals were hotbeds of infection that greatly decreased a patient's chances of successful recovery. All operations which involved opening the abdomen were exceedingly dangerous, and many operations for troubles that would terminate fatally if allowed to take their natural course, were almost certain to result in death at the hands of the surgeon. At the present time a great many of these operations are shorn of their former terrors. The great boon of antiseptic surgery, which has saved literally millions of lives and untold suffering, was a direct outgrowth of the development of our knowledge of the life history of micro-organisms and their rôle in fermentation and decay.

The theory that infections and epidemics are due to minute living organisms brings the phenomena of communicable diseases into relation with other biological facts. Here in a box of apples is a rotten apple which is found to have started decay in others with which it was brought into contact. If we should examine a bit of the decayed apple with the microscope, we should find it teeming with micro-organisms. The power of decay spreads like a disease from one apple to the next. If we take a drop from a fermenting cask of wine and introduce it into thoroughly sterilized grape juice, the latter will begin a fermentation which can be communicated in a similar way to any amount of new fermentable material. Robert Boyle was right. The communication of disease is essentially like the transfer of fermentation from one vat to another.

Many of the early studies on the possible relations of germs to disease were made in connection with anthrax, or splenic fever, which is a highly fatal and contagious malady of cattle and sheep. In 1850, Davaine and Royer had seen small, rod-shaped bodies in the blood of animals dying of anthrax, but they attached no great significance to their observation. The studies of Pasteur led Davaine to renew his investigations, and in 1863 he proclaimed these rod-shaped bodies, or bacteria, as he was the first to call them, to be the cause of the disease. This announcement was received with much skepticism, especially as it was claimed that these bacteria could not always be found in the blood of animals dying of anthrax. Among those who directed their attention to the problem was a young German doctor, Robert Koch, who undertook to grow the bacilli of anthrax in blood serum and aqueous humor. Koch found that the bacteria would multiply in these media and that new drops could be infected from previous cultures for several successive transfers. After eight such transfers, he found that the culture was capable of causing anthrax when injected into healthy mice.

At that time the association of bacteria with disease, which had been observed in a few cases, was interpreted in different ways. Many medical men claimed that bacteria merely accompanied diseases without producing them—the effect of disease instead of its cause—the real causative agent being some substance which was developed in the tissues and blood of the infected animal. Koch's experiments might be interpreted as merely diluting this something without entirely getting rid of it. At this juncture Pasteur was led to attack the problem, which he did with his usual thoroughness. Finding that the bacillus of anthrax would grow readily in sterile urine, he inoculated a large amount of the culture fluid with a drop of blood from an animal affected with anthrax. When this fluid was swarming with the bacilli, he inoculated a fresh lot of fluid with a drop of the culture. With a first dilution of one part to a thousand, the second would be one to a million, and the third, one to a billion. After ten dilutions the original material would be attenuated more than a drop

dispersed in the ocean, but the experiment was continued until forty successive cultures had been made. Since atoms and molecules are not infinitely small, but have a measurable size, it is not probable that even an atom of the original culture fluid was present in the final material used for inoculation. Nevertheless, as Pasteur proved, a drop of the final culture medium, when inoculated into a rabbit or guinea pig, acted in full virulence in producing all the characteristic symptoms of anthrax.

Here is what might be called a crucial experiment. It was no longer possible for opponents to claim that the bacilli of anthrax are the effect of the disease instead of its cause. The same rigid methods of demonstration were applied to the elucidation of the causes of several other diseases. Robert Koch demonstrated conclusively that tuberculosis was caused by a rodlike organism, now known as the *Bacillus tuberculosis*, and he laid down four criteria which should be fulfilled before a given micro-organism is proven to be the cause of a particular disease, instead of a mere accompaniment of it. These were as follows:

1. A particular kind of micro-organism should be found in the blood or tissues of the diseased animal.
2. The organism should be grown outside of the body and obtained in pure culture.
3. The pure culture should produce the same disease when inoculated into a healthy animal.
4. The organism should be found in and recovered from the body of the diseased animal which was inoculated.

These are exacting requirements, but they have been fulfilled in the case of many diseases.

That the discovery of the causes of phenomena is a natural prelude to their control has in no case been more forcibly exemplified than in the history of the germ theory of disease. While experimenting on the germs of chicken cholera and endeavoring to test whether the minute organisms which he was able to cultivate in a nutrient solution would produce this disease if injected into a healthy fowl, Pasteur hit upon a discovery of the

greatest importance for the future of medical science. Happening to inject several fowl with the germs of some cultures which had been allowed to stand for quite a long period, he observed that the injection produced only slight symptoms of the disease. About to throw the cultures away as worthless, he inoculated the same fowl with fresh virulent material, and found to his surprise that they failed to develop the usual symptoms. What was the explanation? Pasteur conjectured that the fowl inoculated by the old cultures had been rendered immune to attacks by more virulent baciili, and he soon convinced himself by further experiments of the correctness of his surmise. Here, he thought, was probably revealed the secret of the success of vaccination against smallpox, discovered by Jenner in 1796. Pasteur was led on to test the efficacy of similar procedures with other diseases. He tried to attenuate the germs of anthrax and succeeded in perfecting a vaccine which could be inoculated into healthy animals without danger, and which protected them against a subsequent inoculation of virulent germs of the same disease. The principle of the attenuated virus, once established by these experiments, has been extensively applied with most beneficial results in the protection of animal life against many maladies.

Pasteur's greatest triumph in the application of this principle was his conquest of hydrophobia. This disease was known to have a uniformly fatal termination if it had once gained a foothold in the body. Suspecting that the disease had its seat in the nervous system, Pasteur proved that matter from the brain of a rabid animal was unusually potent in causing rabies, when injected into guinea pigs and rabbits, especially when it is introduced directly into the brain. Being unable to cultivate the germ of hydrophobia in the usual manner, or in fact to observe it at all, Pasteur attempted to weaken the virus of the disease by drying the spinal cord of infected rabbits. From a spinal cord dried for fifteen days under sterile conditions, a preparation was made which, when injected into healthy animals, proved to be harmless. Then the inoculated animals were given a dose of a preparation which had not been kept so long. After a number of

treatments with preparations of decreasing age, the animals were inoculated with the unmodified virus of a rabid animal. It was found that the treated animals were protected against hydrophobia. The same treatment at first applied to rabbits was found to be equally successful with dogs. Moreover, it was shown that with dogs already bitten by a rabid animal the inoculation had the result of preventing the development of the disease. The success of the protective inoculation, when applied after infection, is rendered possible on account of the fact that hydrophobia has an unusually long period of incubation. The immunizing processes set up by the preparations are fortunately able to produce their effect before the slow march of the deadly virus allows it to gain the ascendancy.

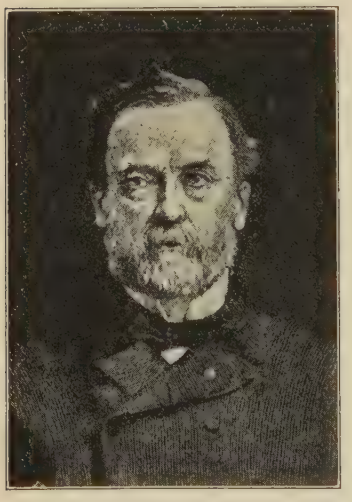

FIG. 37—Louis Pasteur.

The success of the Pasteur treatment in saving the lives of animals raised great hopes of its possible application to human beings. And the results of these applications, when they were finally tried, justified all reasonable expectations. The records of the Pasteur Institute in Paris, where thousands have been treated after being bitten by rabid animals, show that the mortality of treated cases is less than one per cent. Where the bites of the rabid animal are very severe, and especially where treatment has been delayed for several days, as has often occurred, the chances of escaping this fearful malady are greatly reduced. But where treatment is promptly applied and given a fair chance, it almost invariably proves to be successful. There can be no doubt that it has saved many thousands of human beings from one of the most terrible forms of death.

The inoculations for chicken cholera, anthrax, and hydrophobia

owe their efficacy to the development by the body of a power of resistance caused by the introduction of micro-organisms in a weakened or attenuated state. It was formerly held that these weakened organisms used up certain substances in the body, which, while occurring in minute quantities, are nevertheless necessary for their growth. If more virulent germs of the same kind subsequently gain entrance, they find an impoverished soil in which to grow, and hence are unable to thrive. This is a very plausible theory, but it has been shown that it is doubtless incorrect. The secret of immunity has been found to depend in all probability upon quite different mechanisms.

Some animals enjoy what is called a natural immunity. The goat does not readily contract tuberculosis, although most other mammals and even birds are susceptible to some form of this disease. The wild house mouse is protected against pneumonia, which is easily contracted by its albino relative. Some of the races of man are much more susceptible to certain diseases than other races, and even individual members of a race vary greatly in their susceptibility to such diseases as diphtheria, scarlet fever, and measles.

What is called acquired immunity may be brought about in several ways. After recovery from scarlet fever, measles, smallpox, mumps, or whooping cough, the patient rarely suffers a second attack, but there are many other maladies, such as influenza and pneumonia, which do not possess this redeeming quality. In most of the germ diseases, the invading organisms, provided they do not kill the patient, are sooner or later overcome by the defensive reactions of the body, and disappear. There are some maladies, among which are tuberculosis, syphilis, and leprosy, that hang on indefinitely, and still others which, when once started, proceed inevitably to a fatal termination. Immunity, therefore, when acquired at all, is something which is subject to much variation with different diseases. It is one of the fundamental forms of adaptation which is probably possessed in some form by all organisms. Upon what does it depend?

One of the explanations of immunity which has enjoyed a

wide acceptance, especially for several years after it was first announced, is the theory of phagocytosis, developed by Metchnikoff. This theory is based on the observed fact that the white blood cells, or phagocytes, engulf and digest bacteria. There is much evidence that they devour not only dead bacteria, but living ones as well. They are, therefore, defenders of the body against invasion. They frequently congregate in regions where an infection has gained a foothold. There is hence a battle between the organism and its invaders, and many invasions are doubtless checked in their incipience. There is no doubt that the brilliant researches of Metchnikoff have proven that the leucocytes perform an important service in protecting the body against the spread of infection. But there is also no doubt that the theory of phagocytosis alone does not suffice as a general explanation of immunity.

A great part of the progress that has been made in the study of immunity is based upon the information that has been gained as to how bacteria produce their harmful effects. One might easily infer that the bacteria in our blood and tissues would at least do us no good, even if they only cluttered up our physiological machinery by their mere presence. But they do much more than this. When a typhoid patient has a fever, with a splitting headache, and feels as if existence under the circumstances is the very last thing to be desired, it shows that his small bacterial invaders are doing more than taking up space in his body or depriving his cells of a certain amount of nutriment. There is much evidence that disease symptoms result from an actual poisoning. A few kinds of bacteria are known to produce virulent poisons, which can be separated by filtration of the culture medium in which the bacteria are grown. The first clear case of this was furnished by the bacilli of diphtheria. The bacilli of diphtheria, first observed by Klebs and cultured by Löffler, were shown by Roux and Yersin (1888–89) to produce a soluble substance, which, when freed from the bacteria and injected into the blood of an animal, produced many of the characteristic symptoms of diphtheria without, of course, causing the actual disease.

Some strains of the diphtheria bacillus produce a toxin of such virulence that .001 cc. of their filtered culture medium is sufficient to cause the death of a guinea pig. The toxin produced by the tetanus bacillus is excessively poisonous, 0.000005 cc. of a broth culture sufficing to kill a mouse weighing 10 grams. The *Bacillus botulinus*, which has been shown to have caused several deaths from food poisoning, produces a very deadly toxin. Like the tetanus toxin, it manifests a special affinity for nervous tissue, and like it also, it is readily destroyed by heat.

With most pathogenic bacteria, it has not been found possible to demonstrate the presence of soluble toxins. It has been supposed that the toxins are not liberated during the life of the bacteria, but are stored up as endotoxins and set free only when the organisms die and become disintegrated. Since the amount of toxin produced by a given species of bacillus may be caused to vary greatly under different external influences, it has been supposed that many kinds of bacteria generate much more toxin within the body than when grown in an artificial culture medium. However these toxins are produced, there are many facts that indicate that micro-organisms cause their injurious effects by the generation of poisonous substances.

The demonstration of the toxic effects of the diphtheria bacillus formed the starting point of a series of most important discoveries. Prominent among these was the demonstration by Behring and Kitasato of the existence of an antitoxin which has the effect of neutralizing the poison produced by the bacilli of diphtheria. As now perfected, the common procedure of obtaining diphtheria antitoxin in large quantities is to inject into the blood of a horse a sterile solution of the toxin obtained from a culture of the diphtheria bacillus. After a series of such injections, some of the blood is withdrawn from the animal and then freed from its corpuscles and coagulum. The remaining serum is found to contain a substance which neutralizes the poisonous property of the toxin of diphtheria. This may be proven by taking a certain quantity of the toxin, which was previously found sufficient to kill a guinea pig, mixing it with the required

amount of serum from the horse, and then testing its poisonous qualities by injecting it into a guinea pig's blood. If a sufficient amount of the antitoxin is added, the preparation becomes quite harmless. The antitoxin apparently combines with the poison so that the latter has no injurious influence. Soon after its discovery, antitoxin was successfully applied in the treatment of diphtheria in man. Diphtheria is a highly dangerous and treacherous disease. The mortality before the antitoxin era, according to Osler, was from thirty to fifty per cent of affected cases, but it has since undergone a marked reduction. If antitoxin is administered early in the course of the disease, the death rate is exceedingly low.

The method of serum therapy which proved so successful in diphtheria has been applied to other diseases. An antitoxin for tetanus has been obtained in horse serum by following essentially the same method employed in making the antitoxin for diphtheria. This substance was shown to be of great value as a preventive against tetanus during the Great War.

A somewhat different method of combating diseases consists in the employment of a preparation of the killed germs of the disease to be attacked. This is the procedure in the now familiar vaccination for typhoid fever. The bacilli of typhoid fever are grown in a suitable culture medium and then killed by heat or antiseptics. A few injections of the vaccine have been found to protect the body for one or more years against the usual sources of infection, but the immunity, as in some other cases, may be broken down if an extraordinarily large number of typhoid bacilli are taken into the system. The success of typhoid inoculation has been remarkable. The typhoid death rate of inoculated soldiers during the Great War was exceedingly low, even when the soldiers were stationed in typhoid-infested regions. This record presents a striking contrast to that of the Spanish War, when many more soldiers died of typhoid fever than were killed on the battle field. Through the combined influence of vaccination, the purification of water supplies, and efforts to trace and stamp out sources of infection wherever they arise, the

general death rate from typhoid has undergone a very great decrease during the last two decades.

The inoculations which we have considered fall into three classes:

1. Inoculation with living, but weakened, strains of the disease-producing organisms, thereby causing the body to develop its own defensive antibodies. This method is employed in smallpox, anthrax, and hydrophobia.

2. Injection of an antibody so as to neutralize the toxins produced by the organism causing the disease, as is done in diphtheria.

3. Inoculation with the dead germs of the disease, or their products. This causes the body to produce antibodies, by which it acquires a certain degree of immunity. An illustration of this method is furnished by typhoid fever.

These various methods all depend upon the same fundamental principle—the power of an organism to protect itself against toxins by developing some sort of antagonistic substance. The ability of the body to react in this way, however, is not unlimited. There are many poisons to which no immunity can be developed, and there are several diseases which confer no immunity, and against which serum therapy appears to be of no avail. Most of the progress made in the cure of bacterial diseases has been accomplished by taking advantage of the general tendency of organisms to react to injurious substances by the manufacture of defensive chemicals. Getting the better of disease germs is one of the many kinds of adaptive response by which living beings are always meeting the vicissitudes of life. Every germ disease involves a battle in which the body, with its phagocytes, its antibodies, and all the rest of its fighting equipment, endeavors to exterminate the hosts of its little poisonous invaders, which are bent on getting their living at its expense. Now the battle is won by the body, and now it may be won by the invaders, but the fortunes of war depend to a considerable extent upon the condition of the body at the time it enters the contest. It is a well recognized fact that resistance to disease may be greatly reduced by exhaustion, malnutrition, cold, bad air, or any other

agency which impairs general vitality. The domestic fowl, which is ordinarily not susceptible to anthrax, may be caused to contract this disease, as Pasteur proved, if it is chilled by being kept in cold water. It is a common experience that we are more apt to pick up one of those obscure infections called colds if we are run down, fatigued, or harbor some focal infection, such as diseased tonsils. If we would overcome all of our minute, unseen foes, which may find lodgment in our bodies, it is therefore of great importance to keep our chemical defenses in good working order. If the bacteria are poisonous to us, we are likewise poisonous to them, and we are probably more poisonous to them the less poisonous we are to ourselves.

The other great element in the battle, as in battles in general, is the nature of the attacking forces. It would be the height of folly to suppose that even the healthiest body were adequately fortified against all kinds of invaders. Against some of them we are absolutely helpless. Tetanus, anthrax, bubonic plague, sleeping sickness, and rabies apparently pay little attention to any resistance we can make to their progress, once they gain a foothold. With such disease germs, and in fact with all disease germs, the wisest plan is to keep them from getting into the body at all. It is much better to kill them off before they get a chance to enter, or, failing in that, to contrive some way of dodging them. A knowledge of the whereabouts and peculiarities of our bacterial foes helps us immensely in doing both of these things. Here is where, thanks to the remarkable progress of bacteriology, we have a tremendous advantage over our predecessors.

"'Tis the Destroyer, or the Divil," wrote Cotton Mather in 1693, "that scatters Plagues about the World; Pestilential and Contagious Diseases 'tis the Divel who do's oftimes Invade us with them. 'Tis no uneasy thing for the Divel, to impregnate the Air about us, with such Malignant Salts as meeting with the Salt of our Microcosm, shall immediately cast us into that Fermentation and Putrifaction which shall utterly dissolve All the Vital Tyes within us. . . . And when the Divel has raised those Arsenical Fumes which become Venomous Quivers

full of Terrible Arrows, how easily can he shoot the deleterious Miasms into those Juices or Bowels of Men's Bodies, which shall soon Enflame them with a Mortal Fire!"

From this point of view, efforts at sanitation would be in vain, for the "divel" would probably pay scant respect to such things as antiseptics, quarantines, and the purity of water supplies. Nowadays, through knowing the cause of epidemics which, like the cholera and the plague, formerly swept away thousands in their course, we are able to check these diseases before they have fairly started. The average duration of human life is about fifteen years greater than it was half a century ago. Some diseases, such as yellow fever, have been almost completely exterminated. Surgery has been robbed of the worst of its dangers. Infant mortality has been more than cut in half. Cures or preventives have been discovered for some of the most deadly diseases, and the spread of most infectious diseases from person to person has been greatly checked. A large part of this great achievement of science has been the direct outgrowth of our knowledge of the world of microscopic life.

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CHAPTER VII

THE GREEN PLANT

Out of the group of one-celled organisms that we have been considering have arisen two great diverging branches of the tree of life which have culminated in the higher green plants on the one hand and the higher animals on the other. Why life as it developed should have followed just two main paths, instead of many, or only one, is not apparent. Possibly life may have branched out quite differently in other worlds. We do not know. It is evident that without the green plants animal life could not have made a great deal of headway on our planet; but while plants receive benefits in several ways from the presence of animals, they are by no means as dependent on animals as the latter are dependent upon plants. The green plant is the laboratory in which is manufactured food that supports practically all the higher terrestrial forms of animal life. The student of general biology, therefore, cannot well afford to omit the green plant from his program of study.

Since an understanding of the life of a plant depends upon a knowledge of the way in which it is organized, we shall consider first some of the general features of plant structure. A typical green plant consists of three main subdivisions: root, stem, and leaves. The root fixes the plant in the soil and absorbs the water and salts needed for its life; the stem supports the leaves and flowers, and serves as a channel for the transportation of the substances required for growth. The leaves function as organs of absorption and transpiration, and of the synthesis of food materials under the influence of light. In adaptation to their peculiar functions, leaves commonly consist of a thin expanded part, or blade, which presents a relatively large surface exposed to light and air, and a petiole, or stalk of attachment, although

the stalk is not infrequently absent, as in sessile leaves, whose blades are joined directly to the stem. If we make a cross section through the blade of a typical leaf, we shall find that it includes only a few layers of cells. There is an outside epidermis, consisting generally of a single layer of thin cells usually devoid of

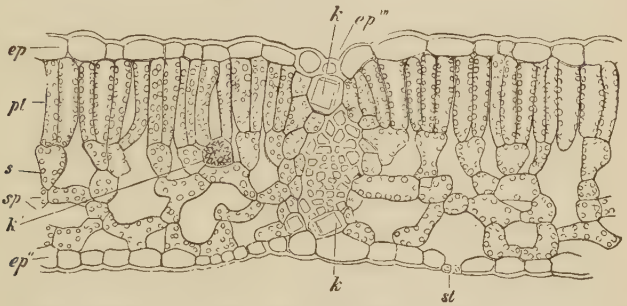

FIG. 38—Cross section of the leaf of Fagus showing different kinds of cells: *ep*, epidermis; *k*, crystals included in some of the cells; *pl*, palisade cells; *s*, *sp*, cells of the loose parenchyma with spaces between them; *st*, stoma, or opening through the lower epidermis. (After Strasburger.)

chlorophyll. In the epidermis of the lower side of the leaf there are, at intervals, peculiar pairs of cells called the guard cells, more or less semicircular in outline, surrounding an opening, or stoma. Through alterations in form, brought about by changes in turgor, the guard cells may open or close the stomata between them and thus regulate the freedom of communication between the interior of the leaf and the outside air. The epidermis is often furnished with hair cells, which are sometimes long and fleecy, as in the leaves of the mullein, and sometimes short and stellate, or occasionally sharp and stiff, as in the nettle. Hair cells very commonly protect the surface of the leaf from too rapid evaporation.

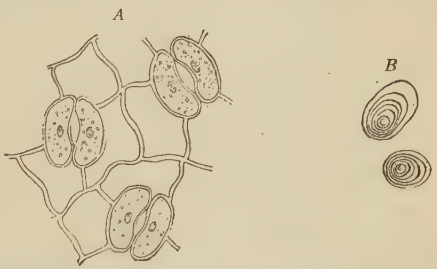

FIG. 39—*A*, stoma cells from the lower epidermis of a leaf with an opening (stoma) between them. *B*, starch grains showing concentric layers.

Just below the upper epidermis the cells (palisade cells) are usually elongated and placed closely side by side at right angles to the surface; below this layer the cells are more loosely arranged with air spaces between them. The thin-walled cells making up the body of the leaf belong to the tissue called parenchyma, as contrasted with the woody fibers and vascular ducts. This rather loose parenchyma is supported by a framework of stronger fibers constituting the so-called veins. In examining a leaf of an oak, apple, blackberry, or Begonia—a very large number of leaves show essentially the same arrangement—several larger veins may be seen diverging from the central axis, or midrib, and giving off branches which divide and redivide, forming a network of supporting tissue. These veins are composed of so-called fibrovascular bundles, and they act not merely as a supporting skeleton for the looser tissues of the leaf, but as conducting channels for the transfer of sap.

The fibrovascular bundle is a sort of unit of composition, out of which a large part of the permanent tissues of the plant is constituted. Each such bundle contains one or more ducts which consist of elongated cells placed end to end. When the duct is fully formed, the cells are dead, and the cross partitions, where the cells meet, have disappeared, thus affording a continuous passage for the transfer of fluid. The walls of these ducts are often marked with pits, rings, or a spiral thickening of cellulose. Alongside the ducts are several elongated tapering cells, with relatively thick walls. These cells (which give the toughness and hardness of woody tissue) together with the ducts, constitute the xylem, or woody part of the bundle. Another part, the phloëm, or bast, lying on the outer side of the bundle, consists mostly of elongated cells (bast tissue) among which are the so-called sieve-tube cells. The latter are arranged end to end, the contiguous ends being perforated by several apertures, which permit the passage of fluids from one cell to the next. Between the xylem and phloëm, is a layer of younger, relatively undifferentiated cells, the cambium, which forms a growing layer, from which cells are added to both of the other groups.

The stems of the higher, or flowering, plants fall into two classes as regards the arrangements of the fibrovascular bundles. In the endogenous stems, exemplified by such plants as the palm and Indian corn, the woody bundles are scattered through the parenchyma, or pithy part of the stem. In the exogenous stems, which occur in most trees, and in the majority of flowering plants, the pith forms a central core surrounded by the wood. The latter is formed from the inner, or xylem, portion of a large number of fibrovascular bundles, closely packed together. The bark is formed from the outer part of such bundles, the cambium of adjacent bundles constituting a continuous layer around the stem. As the cambium is the layer of actively dividing and growing cells, it adds new layers to the outside of the wood and to the inside of the bark. In a cross section of a tree there may be seen the concentric rings of woody deposit marking the stages

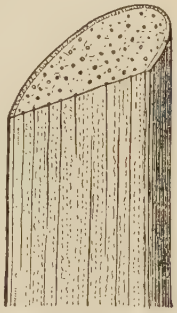

FIG. 40—A section of a stalk of Indian corn showing fibrovascular bundles in the pith. A typical endogenous stem. (After Gray.)

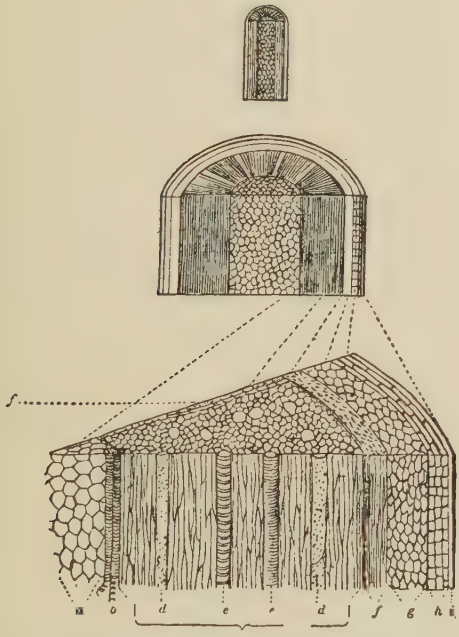

FIG. 41—Section of an exogenous stem of a year-old maple under different degrees of magnification: *a*, central pith; *b*, spiral ducts; *d*, pitted ducts; *e*, annular, or ringed ducts; *f*, inner bark; *g*, green bark; *h*, layer of cork; *i*, epidermis. The *f* on the upper side of the figure represents a medullary ray. (After Gray.)

of annual growth. There are corresponding layers in the bark. In older trees the outer dead layers of bark may be sloughed off or crumbled away, but many annual layers may commonly be seen. At the growing tip of the stem, or its branches, the cells are of the unspecialized or parenchyma type, but most of them which go to form the tissue of the wood or bark become elongated and differentiated structurally in various ways. The fibrovascular bundles found in the leaves extend into the stem and become incorporated into the fibrous tissue of the wood and bark.

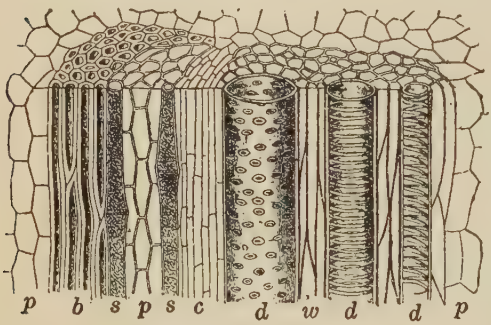

FIG. 42—Section of the stem of a sunflower: *c*, cambium; *d*, ducts of the woody tissue; *b*, bast cells of the bark; *p*, pith, or parenchyma cells; *s*, sieve tubes; *w*, woody cells. (After Wettstein.)

The general structure of the stem is continued into the roots. As the latter subdivide into smaller rootlets, the walls become thinner and more capable of absorbing water. Roots grow in length partly through the elongation of their younger cells, and partly through the multiplication of a group of cells lying just behind a sort of cap of older tissue, which serves to protect the tip as it is pushed through the soil. The surface available for absorption is greatly increased by means of the delicate root hairs which grow out from the outer layer of the smaller rootlets. These hairs have very thin walls in adaptation to their important function of imbibing water with its dissolved salts. As the contents of the root hairs and the outer cells, or epidermis, of the rootlets are more concentrated than the surrounding water, the latter passes by osmosis into the protoplasm of the cells. Most

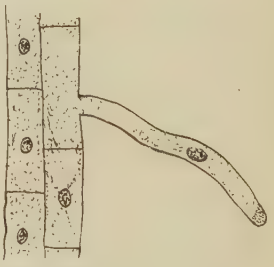

FIG. 43—A root hair growing out from the epidermis of a young rootlet.

of the absorbed fluid passes upward through the ducts of the fibrovascular bundles. This may be demonstrated by suspending young plants so that their roots are immersed in water to which some dye is added that is readily absorbed. After a time the fibrovascular bundles of the stem and even of the leaves will be found to be colored by the dye. While there is not the definite system of circulation in plants that occurs in the higher animals, there is a return flow, whereby the nutrient materials elaborated in the leaves are carried, mainly in the phloëm (which is mostly confined to the inner bark in exogenous stems), to other parts of the plant. This material may flow downward to the roots, or it may pass into the vascular channels of the woody tissue, to be carried upward to nourish the higher growing shoots. It is commonly richer than the inner sap in elaborated food materials, because it contains sugar and proteins manufactured in the synthetic laboratory of the green leaf. The fluids rising from the root contain mainly water and inorganic salts. It is in the green leaves that the raw materials imbibed by the roots are worked up into the more readily assimilable compounds used by the growing tissues.

The formation of carbohydrates in the higher plants occurs in the leaves and green parts of the stem. This synthetic action involves the presence of chlorophyll and takes place under the influence of light. Carbon dioxide, CO_2, and water, H_2O, are brought together in some way so as to form carbohydrates with the liberation of oxygen, O_2. This process, which is known as photosynthesis, includes a number of successive steps, which at present are not clearly understood, but it is supposed by many chemists that the first stage in the process consists in the formation of formaldehyde.

$$CO_2 + H_2O = H_2CO + O_2$$

If formed in the plant cell, formaldehyde does not last long as such. It is convertible into sugar, and is possibly so transformed as rapidly as it is synthesized. Sugar is readily changed by the plant into starch, which is a relatively insoluble carbohydrate of

the general formula $x(C_6H_{10}O_5)$. Starch usually appears in the form of grains composed of many layers surrounding a central body, the layers representing successive depositions of starch to the outside of the grain (Fig. 39, *B*).

By an analogous transformation sugar may be converted into another carbohydrate, cellulose, which constitutes the outer wall of plant cells. In young cells the cellulose wall is thin and elastic, but in the older cells of the wood and bark it may become greatly thickened and rigid. Cellulose is not living tissue. It is a product of cellular activity like the intercellular substance of the connective and supporting tissues of animals. In both plants and animals, the skeletal or supporting structures are composed mainly of extracellular substances.

FIG. 44—A leaf colored in iodine to show the presence of starch. The middle part of the leaf has been covered, to prevent the formation of starch under the influence of light. (After Strasburger.)

In the process of photosynthesis, CO_2 is taken out of the atmosphere and oxygen is given back into it. It is from the atmosphere that plants obtain a large part of the material for their growth. In their dealings with the atmosphere the green plants and animals stand in a reciprocal relationship. Animals take in oxygen and give off CO_2. What is given off by the plant is utilized by the animal and vice versa.

It should be borne in mind, however, that plants perform the function of respiration as animals do, taking in oxygen and giving off CO_2, but this process is masked in the sunlight by the function of photosynthesis. In the dark, plants absorb oxygen and give off carbon dioxide. Respiration is a general function of living matter, whether plant or animal. It goes on in plants, even in the light, side by side with the absorption of CO_2 and the elimination of oxygen. Photosynthesis is a sort of superadded function, the special property of green plants, which gives them their unique and important position in the organic world. In photosynthesis there is an absorption of energy in the form of light.

This makes the green plant a storer of energy; the animal is a spender. The green plants are the great producers of food, the potential energy stored in the carbohydrates, oils, and proteins supplying the energy which is expended in the activities of animals. The heat obtained by burning wood and coal represents the imprisoned energy of sunlight entrapped through the agency of chlorophyll.

The food materials elaborated in the leaves are often stored in other parts of the plant, sometimes in the roots, as in beets and carrots, sometimes in the stem, and sometimes in seeds. In the common potato we have a modified part of an underground stem, which is enlarged and filled mainly with water and starch. Such storage of food frequently subserves the function of tiding over periods of cold or drought. If a potato is planted, its buds, or eyes, form outgrowing stems. The starch is converted into a soluble sugar and employed in the formation of the protoplasm and cellulose of the growing shoot. This transformation of the starch into sugar is really a process of digestion. It is accomplished by a peculiar kind of substance known as a ferment or enzyme.

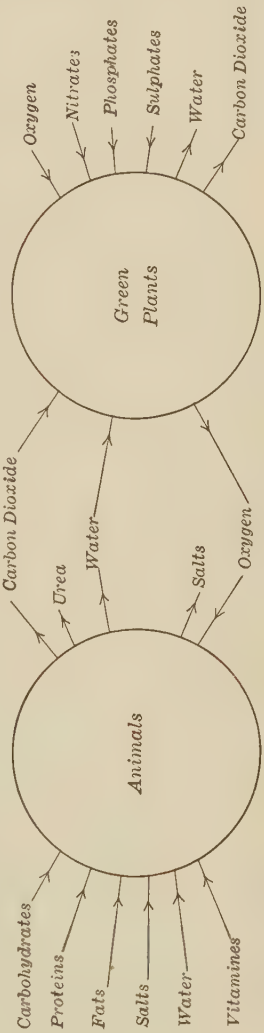

FIG. 45—Diagram illustrating the mutual relationships of higher plants and animals. The arrows indicate the materials taken into or eliminated from the organisms.

Biologists are greatly impressed with the importance of these enzymes in the business of living. There are many kinds of them. Little is known of their chemical composition, or even whether or not they are some form of protein.

They have the property of causing chemical changes in other bodies without suffering much, if any, loss of their own substance. A small amount of enzyme may convert a large amount of other material. Enzymes are not entirely unique in possessing this peculiar property. It is one which is shared by a class of substances known as catalyzers. A catalyzer is supposed to act by accelerating chemical transformations in other substances. Several inorganic substances, among which are platinum sponge and charcoal, possess this power, and they may effect changes in organic compounds similar to those caused by true enzymes. The enzymes act very slowly at low temperatures, and their action is hastened with increase of temperature only up to a certain optimum point, after which it becomes reduced. All enzymes may be destroyed by heat, and most of them are destroyed at 100° C.

Enzymes fall into several classes, according to the kind of chemical transformation which they bring about. The amylases convert starch into sugar; invertase transforms cane sugar into dextrose and lævulose; the lipases transform fats and oils into fatty acids and glycerin; oxydases aid in oxidizing organic substances, especially the carbohydrates, thereby giving rise to free energy; there are several enzymes which attack proteins and convert them into simpler compounds. Ordinary alcoholic fermentation, whereby sugar is converted into alcohol and carbon dioxide, is effected by a ferment produced by the yeast plant. Alcohol may in turn be attacked by another enzyme and converted into acetic acid, as it is in the manufacture of vinegar.

Digestion in animals is mainly the result of the action of enzymes which split up the food materials preparatory to their being absorbed into the body. In plants the nutrient substances usually require no preliminary digestion [1] before being absorbed, since they exist already dissolved in the form of salts in the soil and CO_2 in the air. Digestion in plants is largely employed in order to effect the mobilization of food materials which have been stored in some part in a relatively insoluble form. When digested,

[1] Some of the insectivorous plants digest and absorb the tissues of insects which are caught by devices for entrapping their prey.

the materials may be carried to the place where they are utilized, either in growth or the production of energy.

Fermentation, as commonly observed, is a destructive process, resulting in breaking down compounds into simpler constituents. In recent years it has been found, however, that fermentation may, under proper conditions, result in the synthesis of compounds out of their split products. In other words, the action of enzymes, like a great many other chemical reactions, is a reversible process. Maltase, for instance, ordinarily converts maltose into grape sugar, but if maltase is added to a solution of grape sugar, some of the latter will be converted into a more complex sugar, closely resembling maltose (isomaltose). Enzymes probably play an important part in the constructive metabolism, through which living substances are built up from their simpler constituents, but relatively little is known of the synthetic phases of their action. It is significant that building-up activities which have sometimes been attributed to a special vital force, may, at least to a certain extent, be accomplished through the action of enzymes.

For the synthesis of their protein constituents, the green plants require nitrogen, which they usually absorb in the form of nitrates. They are unable to utilize the free nitrogen of the air or the ammonia, NH_3, which is formed by the decay of organic compounds. The work of converting nitrogen into a form available for the use of the green plant, is performed by bacteria or fungi, as explained in a previous chapter. The life of green plants is, therefore, dependent upon the services of these primitive members of the vegetable kingdom, which in turn derive their subsistence from the decaying bodies of more highly organized types. What is called the nitrogen cycle in the life of plants may be represented by the accompanying diagram. The compounds of ammonia, as well as the free nitrogen of the air, may be converted into nitrites by certain bacteria; the nitrites may be acted on by other bacteria and transformed into nitrates, in which form the nitrogen may be taken into the green plant and used in the formation of proteins. When the plant dies, bacteria destroy

its proteins from which simpler compounds are formed, including nitrates, nitrites, and ammonia. These compounds may be attacked by the denitrifying bacteria, which break them down with the formation of free nitrogen. The nitrogen cycle is thus completed, although the particular series of changes through

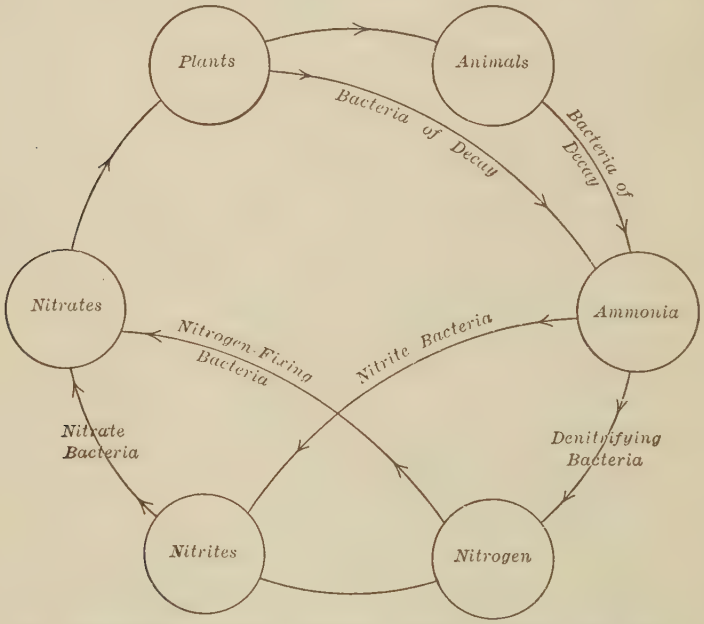

FIG. 46.—The nitrogen cycle and the rôle of different bacteria concerned in the process.

which nitrogen passes in its course from plant to plant is subject to much variation.

Plants require not only nitrogen, oxygen, hydrogen, and carbon, but also sulphur, phosphorus, and often magnesium, potassium, calcium, and iron. Where the products of vegetable growth are continually removed, the soil becomes exhausted, and the required substances must be restored by fertilizers. The natural fertilizers are the remains or the waste products of plants and animals; but minerals, such as potash, Chile saltpeter (sodium nitrate), sulphates, and phosphates, are also employed for this

purpose. To keep up the fertility of the soil, where crops are continually removed, is one of the most important problems of the agriculturalist. With a growing population this problem becomes more and more pressing. A great increase of human population was rendered possible when man began systematically to cultivate plants so as to make them work for him by producing food. The green plant is the source of our life. Man has profited greatly by knowing about its ways and the conditions which favor its best development. The farmer or gardener who knows how to keep on the good side of his vegetable productions by supplying them adequately with nutriment and water, shielding them from the ravages of insect pests and parasitic fungi, and from the destructive competition of undesirable plants, which he calls weeds, will be rewarded by the most abundant yield. Scientific agriculture is one of the mainstays of civilization. Hence the work of agricultural colleges, experiment stations, investigations in soil chemistry and soil bacteriology, the study of forestry, and many other activities, whose aim is to enhance our knowledge of plants as related to human welfare.

We are prone to look upon the life of plants as very different from that of animals, since it appears to be confined almost exclusively to the vegetative functions of assimilation, growth, and reproduction. The great naturalist, Linnæus, expressed our common-sense distinction between minerals, plants, and animals, when he said that minerals grow; plants grow and live; and animals grow, live, and feel. A close study of plant activities, however, shows that plants exhibit a considerable degree of responsiveness to external stimuli. They manifest reactions to gravity by the downward growth of the root and the upward growth of the stem. If a plant is suspended so that the stem points downward, the branches begin to curve and grow upward. That this is not due entirely to the influence of light is shown by the fact that the same phenomenon occurs in plants kept in darkness. It is a manifestation of what is called geotropism. Stems are said to be negatively geotropic because they bend and grow away from the earth, whereas roots are said to be positively

geotropic because they grow toward the earth. If we suspend a bean in a horizontal position in darkness, and keep it supplied with moisture to make it germinate, the primary root, which is first pushed out horizontally, will soon begin to curve downward. The stem which grows out in the opposite direction, soon starts to grow upward against the force of gravity. These opposed modes of behavior are thus manifested by the very first rudiments of the plant body.

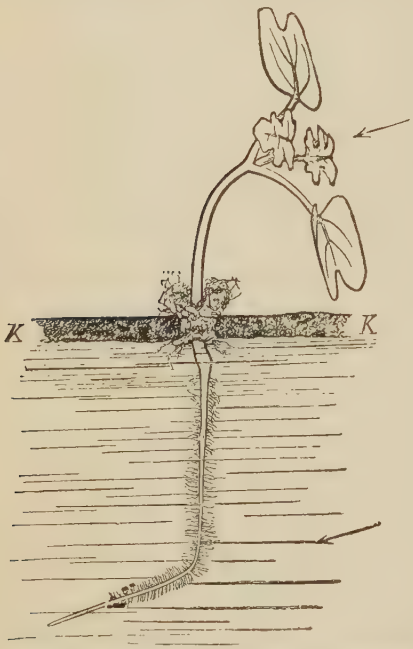

FIG. 47—A seedling of white mustard growing in water and illuminated from the side indicated by the arrows. Note that the stem is turned toward the light, the leaves are at right angles to it, while the root is bent away in the opposite direction. *KK*, a plate of cork in which the seedling is fastened. (After Strasburger.)

Roots in dry soil turn toward regions where they can imbibe the most water. If seeds are allowed to germinate in dry air, and some wet soil is placed near the roots, the latter will turn toward the source of moisture. This is an illustration of positive hydrotropism. That growing plants turn toward the light is a matter of common observation. Grow some seedlings near a window, and you will see their stems bent toward the light, and their young leaves held at right angles to the rays so as to receive a maximum amount of illumination. The stems manifest a fairly simple type of positive heliotropism, or phototropism. The leaves, however, exhibit a peculiar mode of response, inasmuch as they tend to orient at right angles to the rays, instead of parallel to them, as is done by the stems. If you study the arrangement of the leaves of a plant that has been exposed for some time near a

window, you will be able to see that the leaves are held at various angles to the axis of their branches, but that most of them are arranged, so far as is physically possible, in a way that secures the maximum amount of illumination. You will doubtless also be able to observe that the relative lengths of the petioles of the leaves are so adjusted as to give the expanded surfaces the

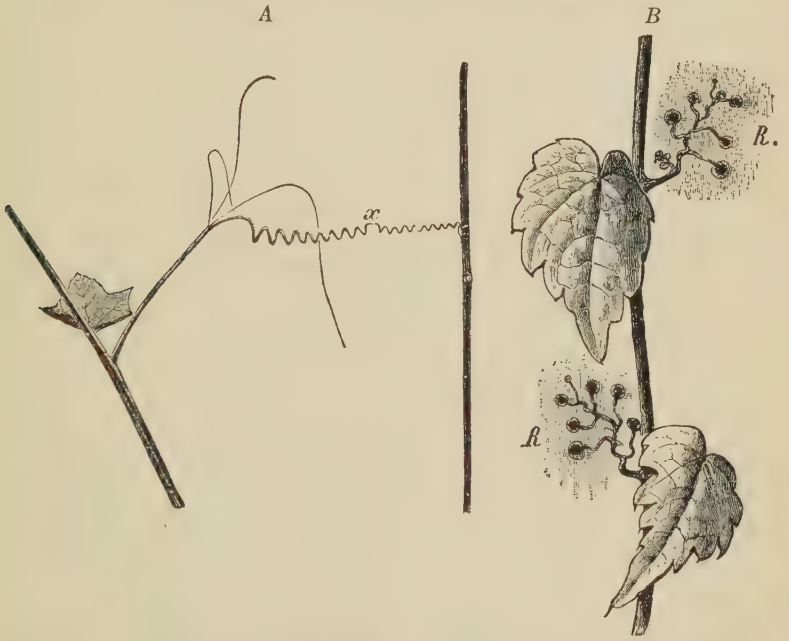

FIG. 48—*A*, tendril from the stem of *Sicyos angulatus* attached to a rod, the direction of the coil reversed at *x*. *B*, part of the climbing stem of *Ampelopsis veitchii* attached to a wall by the expanded tip of its tendrils, *R*. (After Strasburger.)

greatest exposure. Since light is so important in the nutrition of the plant, the adaptiveness of these reactions is obvious.

Plants also manifest very useful reactions to contact. In many twining plants the stem reacts to mechanical contact on one side by curving toward the stimulus. In this way the plant is caused to coil around objects as it grows upward in response to light and gravity. Many climbing plants support themselves by means of their tendrils. Young tendrils, as they grow out as

long slender threads, sway slowly about as if in search of some solid object. In this stage they are soft and flexible, and contain little woody tissue. If a tendril succeeds in encountering a support, it coils around it. In response to the stimulus of contact, woody tissue develops in the tendril which rapidly increases in tensile strength. In many plants the tendrils which do not succeed in meeting with a solid object wither up and die. The Virginia creeper puts out tendrils whose tips, when coming in contact with an object, expand into flattened discs, or suckers. These tendrils, which are more apt to encounter a support on the shaded side of the plant, are negatively phototropic. In a few plants the leaf stalks function as tendrils by actively coiling about twigs of the plant which serves as a support.

FIG. 49—Leaves of the sensitive plant Mimosa. The leaf on the right has responded to a touch by drooping downward and folding together its leaflets. (From Verworn.)

It is not uncommon for plants to fold up or spread out their leaves in response to changes of light or temperature. The so-called sleep movements may be observed in the leaflets of clover and oxalis, which become folded together in the dark but expanded in the light. An extreme irritability is developed in the sensitive plant, *Mimosa pudica*. Even a light touch will cause the compound leaves of this plant to droop downward and the leaflets to be folded together. After this reaction has been evoked several times in close succession, it becomes less readily elicited, as if the plant had become fatigued by its efforts. Claude Bernard discovered that this power of response is temporarily lost if the plant is exposed to the action of ether. "What a singular thing," remarks this writer, "plants can be anesthetized like animals, and absolutely the same phenomena can be observed in the two!"

We are all familiar with the opening of flowers in the morning sun and the closure of their petals in the evening. You may

readily observe this reaction in the heads of a common dandelion. Many flowers—the tulip and crocus, for instance—open when it is warm, and close when it becomes cool. There are specialized responses in several of the insectivorous plants, *e. g.*, the sundew, which enable them to entrap the insects that afford a part of their nutriment. The behavior of these curiously modified forms of plant life is described in an interesting work on *Insectivorous Plants* by Mr. Darwin, who has treated the subject with his customary thoroughness and sagacity.

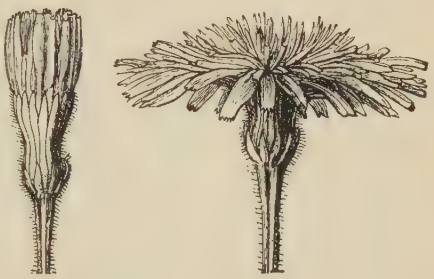

Fig. 50—Flowers of *Leontodon hastilis*, closed in the dark and expanded in the light. (After Detmer.)

All of these activities of plants we have described are the consequences of the irritability of protoplasm. Although they have no nervous system, plants receive and transmit stimuli, and they execute appropriate movements in adjusting themselves to the forces of the outer world. Plants respond to gravity, heat, cold, sunshine and darkness, moisture and dryness, and contact with solid objects in ways which are as appropriate for the maintenance of life as our own responses to a dish of pudding or an automobile coming toward us on the street. If we were so constituted as not to be affected by the pudding (or other aliments) and failed to dodge the automobile, we should not be long for this world. Plants are equally dependent for their continuous existence upon their appropriate behavior. Their life, like that of every living being, is one of continual adjustment.

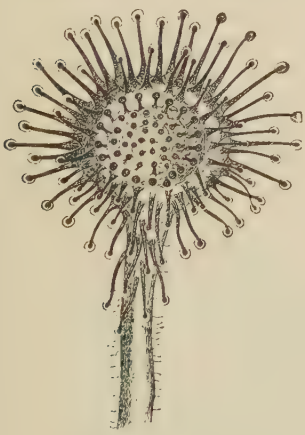

Fig. 51—Leaf of the sundew Drosera seen from above, showing numerous tentacles with expanded glandular tips. (From Darwin's *Insectivorous Plants*.)

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CHAPTER VIII

THE STRUCTURE AND LIFE OF HIGHER ANIMALS

Having endeavored in the preceding chapter to impart some elementary knowledge of higher green plants, let us now make a somewhat similar study of the life of animals. The fundamental life processes in plants and animals, from the simplest one-celled forms to an oak tree or a human being, have very much in common. One organism differs from another largely in the way in which it solves essentially the same problem of getting on in the world and perpetuating its kind. The ways in which the problem is solved are multitudinous; each kind of organism has its own peculiar solution. In some cases it is a relatively simple one; in others it is highly elaborate; but beneath the very conspicuous differences in the ways in which the problem is met by the diatom, the oak tree, the earthworm, and the man of affairs, there are fundamental likenesses in comparison with which most of the differences are, from the viewpoint of the general biologist, relatively superficial.

In considering the elaboration of life processes along the various lines in which it has been carried out, it is well to bear in mind that every living thing is a vortex through which material continually flows. There are, therefore, certain functions, such as absorption, assimilation, respiration, destructive metabolism, and excretion, which are common to all life. Whether we are writing on the life of bacteria or composing a treatise on human physiology, we should be treating of these same functions. A higher animal differs from a very simple protozoön chiefly because it has a number of specialized organs, such as its stomach, heart, lungs, kidneys, muscles, and nervous system, in which to carry out functions which both organisms have in common. The higher animal, of course, does many more things than its hum-

bler relative can, but they reduce themselves to the same general classes.

It will perhaps be advantageous to begin our study of the life of the multicellular animals, or Metazoa, with one of their simpler representatives, the fresh-water Hydra. This common inhabitant of ponds and streams has a cylindrical body about one-fourth of an inch in length, which is usually attached to some object at its lower end, or foot. The mouth, which is at the opposite end of the body, is surrounded by several tentacles, which are remarkably extensile and contractile. These tentacles are adhesive, and are armed with numerous nettling, or poison, cells which poison the small animals upon which the Hydra feeds. Once a hapless water flea or mosquito larva is caught by the tentacles, it is drawn to the mouth and swallowed. The body of Hydra is essentially an elongated sack consisting of two layers of cells, separated by a thin non-cellular lamella, the mesoglœa. The outer layer is known as the ectoderm, and the inner as the entoderm. The former is composed of epithelial cells, whose shape varies considerably in different parts of the body. Some of them are drawn out at the base into a fiber, which is closely applied to the mesoglœa. The fibrous part of the cell is specialized for the function of contraction, the remaining part being much like an ordinary cell of epithelium. These cells are, therefore, called epithelio-muscular cells, and they represent a sort of intermediate stage between an epithelium cell and a muscular fiber. Many of the ectoderm cells, especially on the tentacles, possess peculiar stinging organs, or nematocysts. The latter are elliptical bodies, which contain, coiled up within them, a long thread, which is capable of being discharged with great force. This thread is formed by an inpushing of the outer end of the capsule. When it is discharged it is actually everted, or turned inside out, and in penetrating the tissues of an organism, it introduces some of its contained poison. Since Hydra is, in most respects, a very simple metazoan, it is curious to find that it is armed with cell organs of so highly organized and specialized a kind. Nematocysts are found

in hydroids, jellyfish, sea anemones, and other members of the group of Cœlenterates to which Hydra belongs, but they are not produced by any of the other groups of multicellular animals.

Hydra has no centralized nervous system, but there are several branching nerve cells scattered about under the ectoderm, and there are a few also beneath the entoderm. There are simple sensory cells in both ectoderm and entoderm, which are connected with the epithelio-muscular cells and the nerve cells.

The whole interior of the cylindrical body of Hydra forms the digestive cavity, or enteron. Its lining of entoderm contains many columnar, vacuolated gland cells which secrete the digestive juices that are discharged into the central cavity. Some of the epithelial cells are provided with a flagellum, whose movements serve to keep the contents of the digestive cavity in motion.

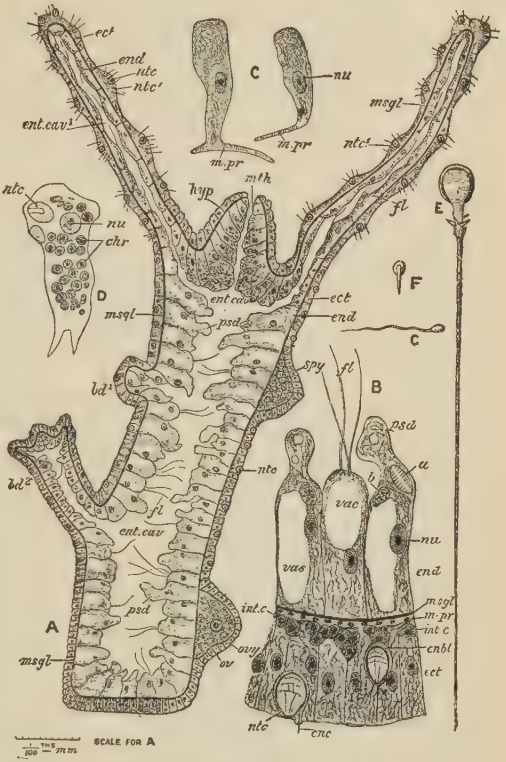

FIG. 52—The fresh-water Hydra: *A*, longitudinal section through the entire animal; *B*, highly magnified section of the body wall; *C*, two ectoderm cells; *D*, an entoderm cell; *E*, a discharged nettling cell; *F*, small nematocyst; *a*, diatom engulfed by an entoderm cell; *bd*¹, *bd*², buds; *chr*, chromatophores; *cnbl*, cnidoblast, or cell containing a nematocyst; *cnc*, cnidocil, or process or a nettling cell; *ect*, ectoderm; *end*, endoderm; *ent cav*, *ent. cav*¹, enteric cavity and its prolongation into the tentacles; *fl*, flagellum; *hyp*, hypostome; *int c*, interstitial cells; *m pr*, muscle process of epithelio-muscular cells of ectoderm; *mth*, mouth; *msgl*, mesoglœa; *ntc*, *ntc*¹, nettling cells; *nu*, nucleus; *ov*, ovum; *ovy*, ovary; *psd*, pseudopodia; *spy*, spermary, or testis; *vac*, vacuole. (From Parker and Haswell's *Zoölogy*.)

The digestive juices of Hydra split up and render soluble the substances taken in as food. Some of the entoderm cells engulf food particles and digest them within vacuoles (intra-cellular digestion), much as is done by an Amœba. The gastric cavity extends into the hollow tentacles, and the products of digestion may be carried into close contact with the cellular layers of these organs.

Hydra has no special organs for circulation, respiration, or excretion. All parts of the body are in a position to take oxygen from and give carbon dioxide and other waste products to the surrounding medium. Hydra is thus devoid of several of the organ systems which make up a considerable part of the body of higher animals. Many of its relatives among the Cœlenterates are more highly organized, but they are all two-layered animals, and are generally lacking in special organs for the functions just mentioned. In the jellyfish, or medusæ, the mesoglœa is greatly thickened and gelatinous in consistency. From the gastric cavity radial canals, usually four in number, extend to join a circular canal situated near the outer margin of the bell, or disc. These canals constitute a sort of distributing or circulatory system, although they are really only extensions of the digestive cavity. In many jellyfish there is a concentration of nerve cells and fibers to form a ring near the margin of the disc, and there are often eye spots, organs of equilibrium (statocysts), and other sense organs developed along the margin in proximity to the nerve ring from which they are supplied with nerve fibers (Fig. 109).

Fig. 53—A piece of red coral showing polyps partly embedded in a calcareous skeleton which is represented in black. (After Lacaze-Duthiers.)

In animals above the Cœlenterates there is a third cellular layer between ectoderm and entoderm known as the mesoderm.

This third layer in several classes of animals is split apart into two layers, one of which becomes applied to the entoderm and the other to the ectoderm. The space between these two parts is known as the cœlom, or body cavity, and it is generally filled with a lymphlike fluid. The surfaces of the cœlom are lined with a thin layer called peritoneum which consists of a thin,

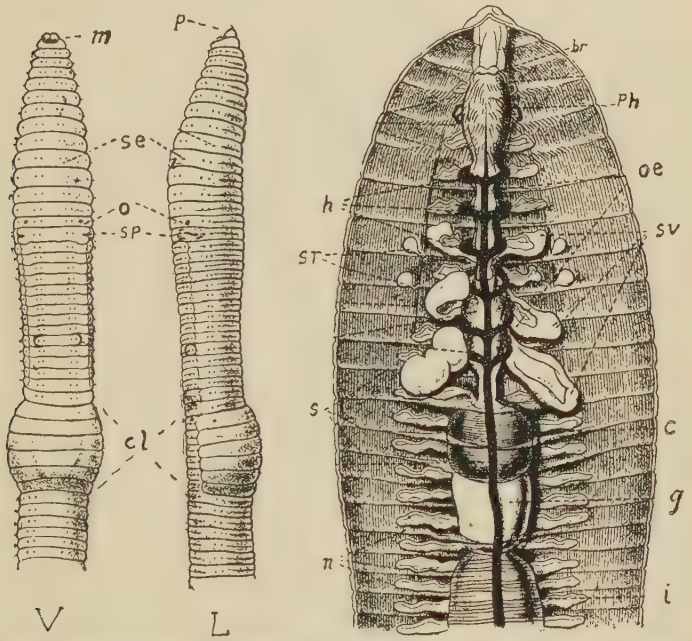

Fig. 54—The earthworm: *V*, ventral, *L*, lateral view of anterior end; *cl*, clitellum; *m*, mouth; *o*, opening of oviduct; *se*, setæ; *sp*, opening of sperm duct. The figure to the right shows the internal organs; *br*, brain; *c*, crop; *g*, gizzard; *h*, hearts; *i*, intestine; *n*, nephridia; *oe*, œsophagus; *ph*, pharynx; *s*, septa; *sr*, seminal receptacles; *sv*, seminal vesicles. (After Hatschek and Cori.)

connective tissue membrane whose free surface is covered with a sheet of epithelium. If we examine the body of an earthworm, we find that it consists chiefly of one tube, the alimentary canal, inside another one formed by the body wall. The inner lining of the inner tube consists of a single layer of entodermic cells. Outside of these are cells of mesodermic origin, forming a muscular coat, and outside of these again, is a layer of peri-

toneum facing the body cavity. In the body wall we find the peritoneum lining the inner surface, then a layer of longitudinal muscle fibers, then a layer of circular muscles, and finally an epithelial layer representing the ectoderm. The latter secretes a thin, non-cellular cuticle of a substance called chitin, which forms a smooth outer covering of the entire body.

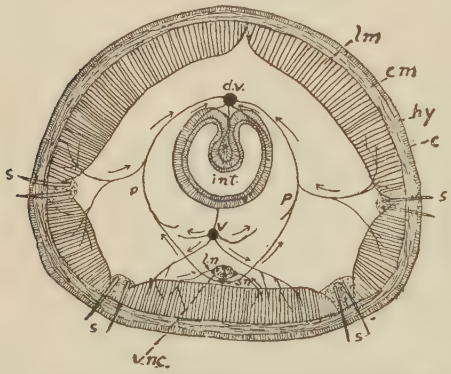

FIG. 55—A cross-section through an earthworm: *c*, cuticle; *cm*, circular muscles; *dv*, dorsal blood vessel; *hy*, hypodermis; *lm*, longitudinal muscles; *ln*, lateral neural blood vessels; *p*, parietal blood vessels; *s*, setæ; *sn*, subneural blood vessel; *vnc*, ventral nerve cord. The arrows indicate the direction of the blood flow.

The cœlom of the earthworm is divided into compartments corresponding to the segments of the body by means of transverse partitions, or septa, extending from the alimentary canal to the body wall. Much the same double-tube arrangement is found in nearly all higher animals. The cœlom may be well-nigh obliterated in many groups, such as the insects, crustaceans, and arachnids, but it is well developed in most annelid worms, in the echinoderms (starfish, sea urchins, etc.), and in the vertebrates.

The digestive tube, or alimentary canal, of higher animals is typically furnished with muscular coats, whose peristaltic, or wavelike, contractions pass normally toward the posterior end of the body. These contractions force the food along the alimentary canal and eventually effect the discharge of the undigested residue. Sometimes there is a specialized part of the alimentary canal which serves for the storage and partial digestion of food, as in the crop of birds.

In digestion, as in many other physiological functions, an important part is played by the organs known as glands. These structures are usually formed by the inpushing of an epithelial layer whose cells become specialized for the function of secre-

tion. In form, a gland may be a simple, cuplike depression, a single tube, or a greatly ramified tubular structure whose branches discharge by a common duct. The walls of the stomach are furnished with simple or sparingly branched, tubular glands which secrete mucus and gastric juice. There are many simple and branched glands in the lining of the small intestine. The liver and pancreas are really glands of large size and complicated structure. The branches of the larger glandular organs are

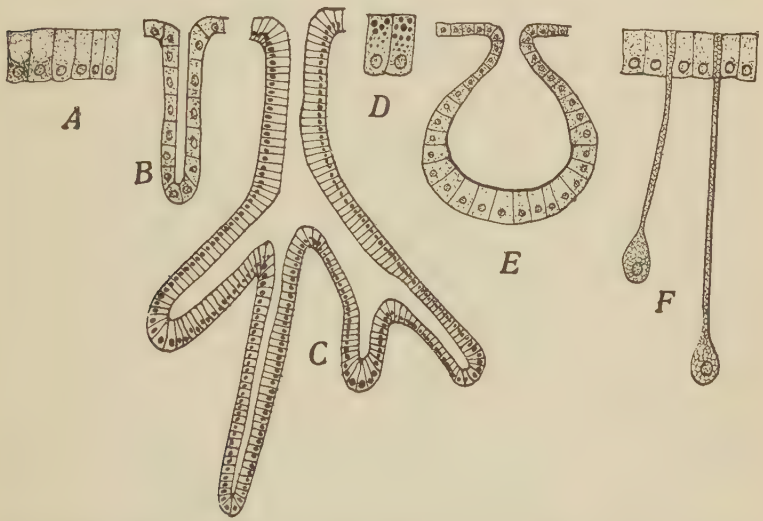

FIG. 56—Types of glands: *A*, two mucus cells in a layer of epithelium; *B*, simple tubular gland; *C*, branched tubular gland; *D*, secreting cells of the pancreas; *E*, saclike, or alveolar gland; *F*, unicellular glands.

held together by a connective tissue framework, which affords a support also to the blood vessels with which the organ is supplied.

The process of secretion, which is the primary function of a gland, is one of the fundamental activities of living protoplasm. It occurs in the endoplasm of an Amœba during the discharge of digestive fluids into the food vacuoles very much as it does in the gastric glands of a human being. Almost all cells may secrete something—in a plant nearly all of them secrete cellulose—but in a gland this general secretory function is emphasized and

specialized. Cells of different kinds of glands, all nourished by the same blood stream, produce very different products; mucus, gastric juice, bile, pancreatic juice, urine, oil, sweat, and many other materials are elaborated by the different glands of our own bodies; while the poison of the rattlesnake, the ill-smelling product of the scent glands of the skunk, the wax of the honey bee, and the web of the spider are some of the very diverse products of secretion found in other animals. Sometimes secretory cells simply eliminate substances already present in the blood, as when urea is secreted by the tubules of the kidney. But in most

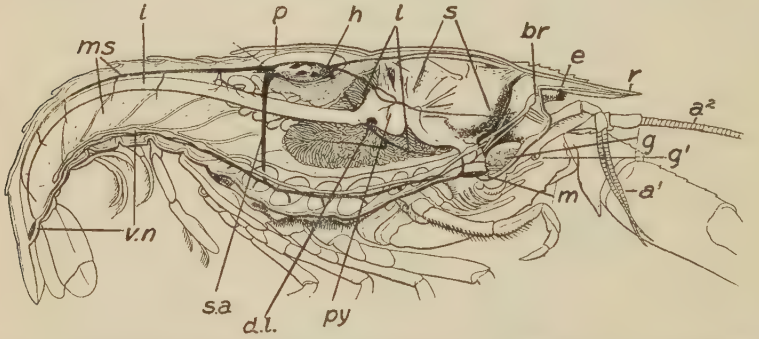

FIG. 57—Longitudinal section through the body of a crayfish: a^1, first antenna; a^2, second antenna; *br*, brain; *d. l.*, duct of liver; *e*, eye; *g*, green gland, or organ of excretion opening at g^1; *h*, heart; *i*, intestine; *l*, liver; *m*, mouth; *ms*, muscles; *p*, pericardium; *py*, pyloric division of the stomach; *r*, rostrum; *s*, stomach; *sa*, sternal artery; *vn*, ventral nerve cord. (After Hatschek and Cori.)

cases, the secretion is a synthetic product of the peculiar metabolism of the gland. The substances secreted by gland cells are generally discharged toward the free end of the cells, while materials are absorbed at the opposite end from the blood or lymph. The mechanisms of absorption and discharge which accompany secretion are as yet inadequately understood, and for an account of the attempted explanations of the phenomena the student must be referred to special treatises on physiology.

What is commonly designated as a stomach in animals is an enlarged part of the digestive tube devoted mainly to digestion. In the crayfish the stomach is furnished with a chitinous lining

which is thickened in places so as to provide hard teeth, or ossicles, for grinding up food. This gastric mill, as it is designated by Huxley in his classical volume *The Crayfish*, is operated by muscles attached to its outer surface. The posterior part of the stomach receives the ducts from a large branched organ, formerly known as the liver, but now, with more discretion, called simply the digestive gland. This gland produces ferments which split up and render soluble both proteins and carbohydrates. It has been found to function also as an organ of absorption, since some of the materials from the stomach make their way into it and are then taken up by its walls. The intestine of the crayfish is a simple, straight tube extending from the stomach to an opening in the last segment of the body.

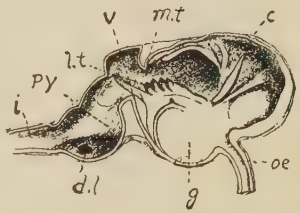

FIG. 58—Section through the stomach of a crayfish: *c*, cardiac region; *dl*, duct from the liver; *g*, gastrolith; *i*, intestine; *lt*, *mt*, lateral and median teeth of the grinding apparatus; *oe*, œsophagus; *py*, pyloric region of stomach; *v*, valve between cardiac and pyloric regions of the stomach. (After Hatschek and Cori.)

In the different groups of vertebrate animals the alimentary canal presents much the same divisions. Leading from the posterior part of the mouth cavity, or pharynx, there is a tubular œsophagus, through which food is passed into the stomach. From the stomach the alimentary canal is continued as the small intestine, which widens abruptly into the large intestine, whose terminal part discharges to the outside of the body. At the juncture of the large and small intestine, there is commonly an offshoot known as the cæcum. In the horse, cow, and most other herbivores, this cæcum is a large and important element of the digestive apparatus, but in the apes and in man it is reduced to a short rudiment, and its terminal portion, the vermiform appendix, is narrowed into a small tube. Near its attachment to the stomach, the small intestine receives the secretion of two large glands, the liver and the pancreas.

In the mammals some of the preliminaries to the process of digestion take place in the mouth, where food undergoes a certain

amount of mastication and at the same time becomes mixed with the secretion of the salivary glands, which contains a ferment having the property of converting starch into sugar. The lower vertebrates, such as the fishes, amphibians, and reptiles, usually dispense with the preliminaries of mastication and swallow their food entire. The teeth of these animals are therefore not fitted for grinding, but are generally sharp and conical in adaptation to their primitive functions of seizing and holding prey. The tongue, which has no independent movement in fishes, is utilized in the Amphibia as an organ for securing food. Being attached at its anterior end, near the tip of the lower jaw, it is capable of being thrust out with surprising rapidity. The secretion which covers its free posterior end causes it to adhere to small insects or worms, which are then quickly withdrawn into the mouth. In the mammals the tongue comes to be an almost indispensable aid in mastication and in swallowing. In man its services have also been enlisted in the aid of an entirely different function of articulate speech. Among the Amphibia, and also the primitive birds and mammals, the tongue is used but slightly, if at all, to modulate the sounds produced by the vocal cords. But in the higher birds, and especially in the higher mammals, this organ becomes one of great importance for the production of the numerous sounds which are of so much significance in the conjugal, parental, and social relations of these animals. In the evolution of the tongue, with all its vast importance in making possible the development of human speech, we have an excellent illustra-

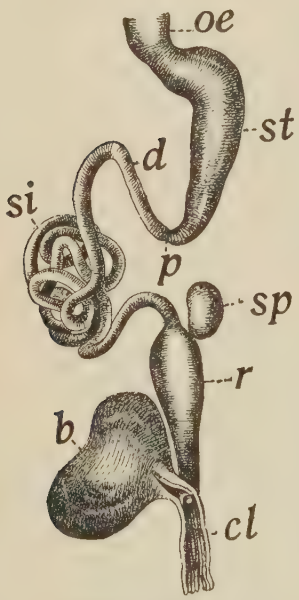

FIG. 59—Alimentary canal of the frog: *b*, bladder; *cl*, cloaca; *d*, duodenum; *oe*, œsophagus; *p*, pyloric constriction at the juncture of the stomach and intestines; *r*, rectum; *si*, small intestine; *sp*, spleen; *st*, stomach. (After Ecker.)

tion of how organs, originally evolved in relation to certain functions, come later to take on quite different uses. It not infrequently happens that the secondary, or derived, function, supplants the original one entirely.

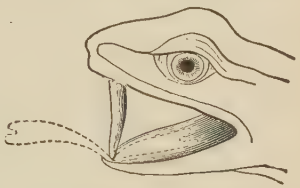

FIG. 60—Tongue of frog. The dotted outlines show different positions in the extrusion of the tongue. (After Wiedersheim.)

When food passes into the stomach, it causes the gastric glands to secrete a fluid called gastric juice. This secretion is acid in reaction, owing to the presence of a small percentage of hydrochloric acid. It also contains a special ferment, pepsin, which requires an acid medium in order to perform its characteristic function, which is the conversion of proteins into simpler, soluble compounds called peptones. There is another ferment, rennin, which coagulates some of the proteins of milk. Starch is not acted on by the gastric secretions, although while in the stomach it may be converted into sugar by the saliva mixed with the food.

When the process of digestion in the stomach has reached a certain stage, the pyloric constriction at the smaller end of the stomach relaxes, and allows the contents to pass into the small intestine. Here the food is acted on by a number of other ferments. Most important of these are the ferments of the pancreatic juice. The secretion of the pancreas, which is alkaline, because of the presence of sodium carbonate, neutralizes the acid contents of the stomach, and thus furnishes a suitable condition for the action of its own ferments, which are most effective in a medium of alkaline or neutral reaction. One of these ferments (steapsin, or lipase) converts fats into fatty acids and glycerin; others convert the carbohydrates which may have escaped digestion by the saliva into sugar (maltose and dextrose); and still another converts proteins into simpler products. The latter ferment, as it leaves the pancreas, is in an inactive form called trypsinogen, but in the small intestine it becomes activated by a secretion called enterokinase, and thereby converted into trypsin, which acts upon the proteins, transforming them finally into

their primitive constituents, the amino acids. The last stages of the reduction of proteins are also brought about by a ferment (erepsin) contained in the fluid secreted by the small intestine. The bile possesses relatively feeble power as a digestive fluid, although it renders conditions more favorable for the action of other digestive juices. To a considerable extent it contains waste products eliminated by the liver.

When, as a result of the action of many ferments, the proteins in the intestine are reduced to amino acids, the carbohydrates to dextrose and other simple sugars, and the fats to fatty acids and glycerin, these products of digestion are ready to be absorbed. The function of absorption is discharged mainly by the small intestine, although a certain amount of absorption may take place in both the large intestine and the stomach. The folds of the inner lining of the small intestine and the minute, finger-shaped villi, which project into its cavity, are devices for increasing the surface through which fluids may be absorbed. The products of digestion diffuse into the blood and lymph, whence they are carried to various parts of the body to be used in building up the different tissues. The sugar which diffuses into the blood mainly as dextrose may be stored up, especially in the liver and muscles, in a relatively insoluble form of carbohydrate known as glycogen, or animal starch $x(C_6H_{10}O_5)$. As Claude Bernard proved in his brilliant investigations on the glycogenic function of the liver, glycogen may be converted by fermentation into dextrose, which, being readily soluble, diffuses into the blood. Normally the percentage of dextrose in the blood is very small. The liver acts as a reservoir of glycogen, storing it up after

FIG. 61—Section of the small intestine of man showing the folds of the inner surface.

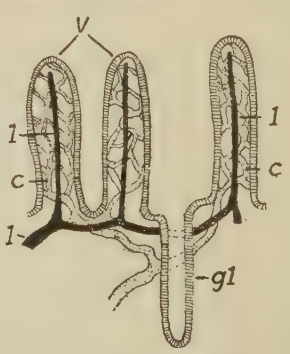

FIG. 62—Villi of the small intestine and their vessels: *c*, capillaries of blood vessels; *gl*, gland; *l*, lymph vessels shown in black; *v*, villi.

a meal of carbohydrates and giving it out slowly into the blood as occasion requires. The rôle of glycogen in the life of an animal is, therefore, analogous to that of starch in the life of a plant.

In the higher animals, as in the higher plants, there has come to be developed a transportation system whereby absorbed food material and oxygen are carried to different parts of the body, and the waste products of metabolism are carried to where they are discharged. In the sponges, Cœlenterates, flatworms, and other lower invertebrate animals there is no definite system of circulation. Such a system is not necessary in forms whose small size or peculiar form makes possible a more or less ready exchange of materials between their tissues and the absorbing or eliminating surfaces of the body. With larger forms having

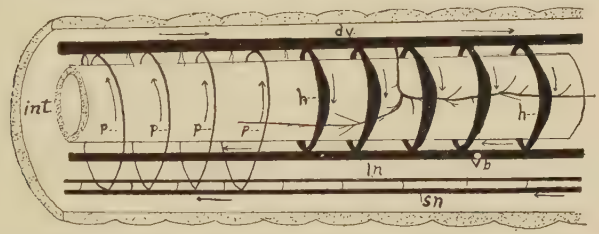

FIG. 63—Lateral view of the blood vessels of the earthworm: *dv*, dorsal blood vessel; *h*, hearts; *int*, intestine; *ln*, lateral neural blood vessel; *p*, *p*, parietal blood vessels; *sn*, subneural blood vessel; *vb*, ventral blood vessel. The arrows indicate the direction of the blood flow.

parts far removed from the sources of food and oxygen a circulatory system becomes a practical necessity. A primitive and generalized form of such a system is found in the common earthworm. There is a blood vessel lying above, or dorsal to, the alimentary canal and a similar vessel lying below, or ventral to the alimentary canal, both of these extending nearly the length of the body. There are three other longitudinal vessels, a single, subneural, and two lateral neural vessels, that lie close to the ventral nerve cord. In the anterior part of the worm five pairs of large vessels, called aortic arches, or sometimes "hearts," extend around the alimentary canal and connect the dorsal with the ventral, or subintestinal, blood vessel. Behind the aortic

arches a series of paired vessels, a pair to each segment, connect the subneural vessel with the dorsal vessel, and receive branches from the body wall. The whole system of circulation in the earthworm is one of closed tubes, and the blood which is red from the presence of hæmoglobin dissolved in the plasma, contains a number of amœboid corpuscles resembling leucocytes. The blood is propelled by the peristaltic contractions of the dorsal vessel, which pass from behind forward, forcing the blood through the aortic arches into the ventral blood vessel, whence it flows backward and is eventually distributed by lateral branches to the body wall, alimentary canal, and various other internal organs. The blood is returned by the pairs of vessels entering the dorsal vessel behind the aortic arches. The circulatory system of the earthworm is furnished with both outgoing vessels, or arteries, and return vessels, or veins, but in the

FIG. 64—Diagram of the arterial arches of a fish: *ar*, aortic arches; *au*, auricle; *da*, dorsal aorta; *v*, ventricle.

crustaceans, insects, arachnids, and molluscs, clearly defined return vessels are not present, the blood finding its way back through irregular spaces, or sinuses, between the tissues.

Among the vertebrate animals the general plan of the circulatory system is apparently quite different from what prevails among the invertebrates. The heart is ventral instead of dorsal to the alimentary canal, and the general direction of the arterial blood flow is forward on the ventral, and backward on the dorsal side of the body. In a fish, such as the common dogfish, or shark, which well exemplifies the typical scheme of circulation in the lower vertebrates, the heart consists of two principal chambers, an auricle which receives the venous blood, and in

front of this the very thick-walled ventricle, which is the main organ for the propulsion of blood through the arteries. The chief veins empty into an enlargement, the sinus venosus, which discharges its blood into the auricle. Between the sinus and the auricle, and between the auricle and the ventricle, are flaps, or valves, which permit the blood to flow anteriorly, but which close upon backward pressure so as to prevent its return. From the anterior end of the ventricle, the ventral aorta extends forward to the gill region, where it gives off five pairs of branchial arteries which supply blood to the gills. The heart contracts from behind forward, and acts much like a force pump in propelling the blood through the arteries and other blood vessels. The branchial arteries supplying the gills subdivide into very small branches, or capillaries, which supply the gill filaments. After passing through these filaments, the blood is collected into larger vessels, which extend dorsally and finally unite to form the large dorsal aorta, which runs backward and supplies most of the organs of the body.

The arteries after branching repeatedly, end in very small, thin walled capillaries, out of which materials diffuse readily into the tissues, and into which waste products from the tissues diffuse readily into the blood. After passing through the capillaries, the blood flows into the smaller veins, and the latter unite to form the larger venous trunks, from which the blood finally is returned to the heart.

An exception to the usual arrangement is found in the blood vessels supplying the liver. In addition to the typical arterial supply which is furnished by the hepatic artery, the liver receives a large amount of venous blood from the portal vein. This vein takes its origin in the capillaries of the stomach, intestines, and adjacent organs, and it also ends in capillaries in the lobes of the liver. It serves to convey some of the products of digestion, especially dextrose and amino acids, directly to the liver, through which they must pass before being carried to other parts of the body. In the lower vertebrates there is an analogous renal portal system which carries venous blood to the kidneys, but,

unlike the hepatic portal system, this arrangement is dispensed with in the higher vertebrates.

The chief differences between the circulatory systems of the higher and the lower vertebrates are due to the fact that the former are typically terrestrial and lung-breathing animals, while the latter are aquatic and breathe by gills. One of the chief functions of the circulatory system is to distribute blood to the organs of respiration, and where these organs undergo a radical change, this inevitably entails changes in the distribution of the blood vessels. The replacement of gills by lungs took place very gradually in the development of higher animals. There are several kinds of amphibians, to say nothing of the so-called lungfishes, which possess both lungs and gills at the same time, and almost all of the amphibians bear gills when they are young tadpoles. One may trace many intermediate stages between the fish type of circulation and the type found in mammals and birds. In the two latter groups the heart consists of four chambers (two auricles and two ventricles) and there is a complete double circulation. The venous blood coming from the organs of the body passes into the right auricle, thence through the tricuspid valve to the right ventricle, and thence through the pulmonary arteries to the lungs. After being oxygenated in passing through the lung capillaries, the blood is returned through the pulmonary veins to the left auricle, whence it passes through the mitral valve into the left ventricle, by which it is pumped through the aorta and its various arteries to the organs of the

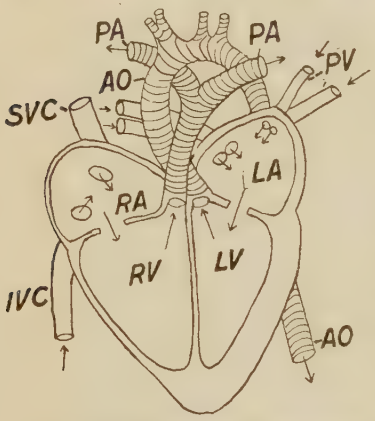

FIG. 65—Section through the mammalian heart: *AO*, aorta; *IVC*, inferior vena cava carrying blood to the right auricle; *LA*, left auricle; *LV*, left ventricle; *PA*, pulmonary artery; *PV*, pulmonary vein; *RA*, right auricle; *RV*, right ventricle; *SVC*, superior vena cava. The arrows show the direction of the blood flow.

body. Here is a scheme of circulation quite different from what is found in the fishes. Nevertheless, in the arch of our aorta, there is a persistence of one of the old aortic arches by which blood was carried to the gills. Most of the other arches are gone, but fragments of them still persist in the pulmonary arteries and parts of other trunks.

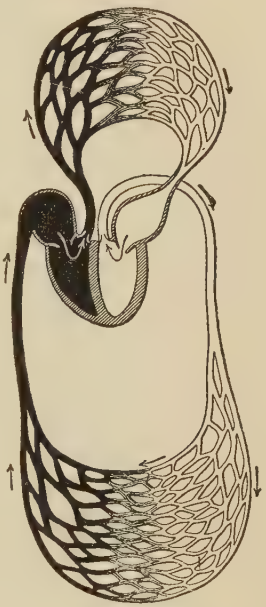

Fig. 66—Diagram of the double circulation, the pulmonary above and the systemic below. The light vessels are those carrying oxygenated blood, the dark ones those carrying venous blood. (From Rathke.)

Specialized organs of respiration, like organs of circulation, are commonly absent in the simpler forms of animal life. They are usually, if not always, absent in sponges, Cœlenterates, roundworms, flatworms, and many of the smaller representatives of other groups. In these forms the exposed surface of the body suffices for the function of respiratory exchange. Even in so highly organized an animal as the earthworm, there are no special organs for respiration, although such organs are found in many of its relatives among the marine annelids. However, it is only when animals are at least not very large that they can get along without organs of respiration. As animals increase in size, such organs are necessitated as a result of mere bulk. This is one of the many biological consequences of the simple geometrical fact that while the surface of an object varies as the square of its diameter, its volume varies as the cube. As objects increase in size, the ratio of surface to volume, therefore, becomes smaller. Since, other things equal, the metabolism going on in an organism varies in pro-

Fig. 67—Capillaries of the frog's foot showing the corpuscles. *p*, *p*, pigment cells.

portion to its volume of living substance, growth beyond a certain size must produce a state in which the entrance and exit of substances through the surface will no longer suffice for the maintenance of life processes. This is true in relation to the absorption of food and excretion, as well as respiration. Hence the coiled intestine of many forms, the inner folds in its wall, and the projecting villi. Hence the branching of glands involved in secretion, and hence also the various devices for increasing extent of surface in organs of respiration.

Respiration involves taking in oxygen and giving off carbon dioxide. This process takes place in all cells of the body, wherever situated. It occurs in parts far removed from any respiratory

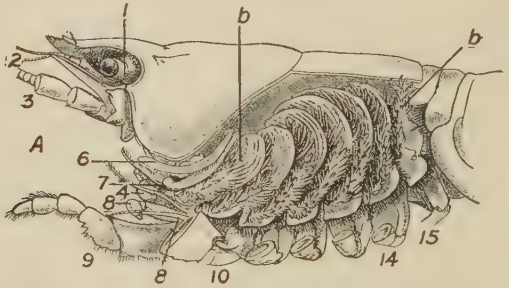

FIG. 68—The gills of the crayfish, which have been exposed by cutting away the covering of the gill chamber: *b*, branchiæ, or gills; *1*, eye; *2*, *3*, first and second antennæ; *6–9*, mouth parts; *10–15*, legs. (After Huxley.)

organ, the oxygen being derived from the blood and the carbon dioxide being given to the blood in exchange. This is called internal, or tissue respiration, as distinguished from external respiration occurring in lungs or gills. In external respiration the exchange is between the blood and the outside air or water. The blood functions, therefore, as an intermediary between tissue respiration and external respiration in carrying oxygen and carbon dioxide, it being especially adapted to carrying oxygen on account of the peculiar properties of its hæmoglobin.

Organs of respiration consist of two kinds of devices. They are formed either by inpushing or outpushing the surface of the body, thereby increasing the area exposed to water or air. In aquatic animals we generally find the outpushings. What are

called gills are usually filamentous or platelike expansions of the body wall. As a moist surface is required for effective gaseous exchange, this condition is fulfilled if the gills are bathed in water. Drying the gills of an aquatic animal usually causes death from suffocation. In terrestrial animals, gills are not usually found, and where they occur they generally have a protective covering, as in land crabs, which shields them from too rapid evaporation.

Among animals inhabiting dry land the increase of the area exposed to air, and its maintenance in a moist condition, are usually secured by inpushings of the surface of the body. In the insects there are tracheal tubes beginning in outer apertures (spiracles) situated at the sides of the body, and ramifying among the tissues of the various organs. These tubes have a thin, chitinous lining, continuous with the general chitinous covering of the body, and marked with a spirally coiled thickening, which serves to keep them continually open. Among insects, air is carried to the blood, instead of blood being carried to the air, as it is in ourselves. In the vertebrates, from the amphibians up to birds and mammals, respiration is carried on by lungs. Some of the amphibia have lungs which are simple sacs connected with the ventral surface of the throat. In others of this group the inner surface of the lung is increased by a series of folds, giving it a honeycombed appearance. In man the lungs represent a highly ramified system of tubes ending in thin-walled air cells whose total area has been estimated to be over one hundred times as great as the outer surface of the body.

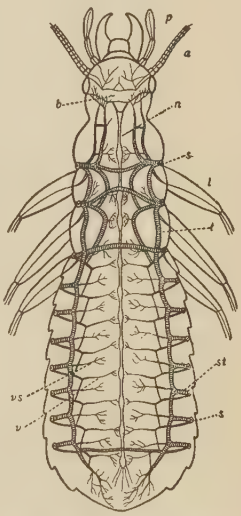

FIG. 69—Tracheal system of an insect: *a*, antenna; *b*, brain; *l*, leg; *n*, ventral nerve cord; *s*, spiracles; *st*, spiracles; *t*, tracheal trunks; *v*, *vs*, branches of tracheal tubes. (After Kolbe.)

Animals with organs of respiration are commonly provided with some mechanism for producing respiratory movements. The crayfish is furnished with a flap attached to one of the pairs

of oral appendages, which moves back and forth so that a current of water is kept flowing through the gill chamber. The abdomen of insects regularly expands and contracts, thus forcing air in and out of the tracheal tubes. Fishes, by means of movements of the jaws and gill supports, take water into the mouth and force it out through the gill slits in the sides of the pharynx. In mammals the air is drawn into and expelled from the lungs by means of the movements of the diaphragm and the action of the muscles which expand and contract the chest. All of

FIG. 70—A shark. The gill slits are shown behind the mouth. (After Dean.)

these activities have as their obvious function the renewal of the air or water in contact with the exposed surfaces, thus facilitating the exchange of gases involved in respiration.

The function of execretion, or the removal of waste products of metabolism, is, like respiration, a general property of living substance. In fact, one part of the process of respiration, the elimination of carbon dioxide, is essentially an excretory process. There may be no definite organs of excretion in the most primitive multicellular animals, the general surfaces of the body sufficing for this function. The prevailing type of excretory system in the lower invertebrates consists of a series of tubules which are commonly branched and terminate in enlargements, whose inner cavity contains a tuft of long cilia arising from the closed end of the tubule. These terminal enlargements generally consist of a single cell, commonly called a flame cell on account of the resemblance of the movements of its tuft of cilia to the flickering of a flame. The beating of these cilia creates a current which carries the products, excreted by the walls of the tubule, to the outside of the body.

In the annelid worms there is generally a pair of excretory organs, the nephridia, in most of the segments of the body. The nephridia are tubules, frequently more or less coiled, which end either in bodies resembling flame cells, or else, as in the earthworm, by a funnel-shaped mouth opening into the cœlom, or body cavity. The funnel is furnished with cilia, whose beating draws the cœlomic fluid into the tubule. The cells of the tubule, which are the most important factors in excretion, discharge their products into the cavity of the tubule, whence they are carried, through a pore in the body wall, to the outside.

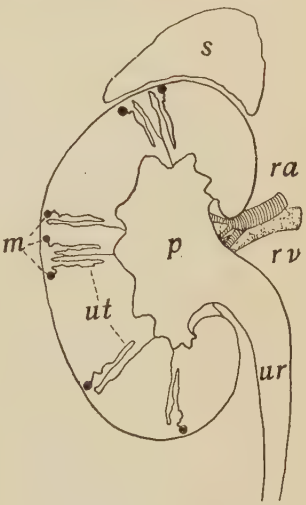

FIG. 71—Diagram of a longitudinal section through a human kidney: *m*, Malpighian corpuscles; *p*, pelvis, or central cavity; *ra*, renal artery; *rv*, renal vein; *s*, suprarenal gland; *ur*, ureter; *ut*, uriniferous tubules.

In the vertebrate animals the chief means of excretion consists of a pair of kidneys. These open through the ureters into the terminal part of the alimentary canal in the lower vertebrates and birds, or else into the urinary bladder, as in mammals. In appearance the kidneys of vertebrates present little resemblance to nephridia, but a study of their finer structure shows that they consist of a mass of coiled tubules resembling, more or less, the individual nephridia of the worms; and in the lower vertebrates the resemblance may be increased by the presence of ciliated funnels, or nephrostomes, opening into the body cavity. Each tubule ends in an enlargement partially surrounding a knot of blood vessels, the glomerulus, the whole structure forming what is called a Malpighian corpuscle. The terminal part of the tubule surrounding this

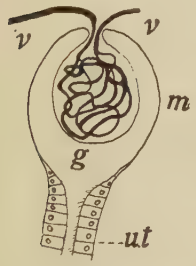

FIG. 72—Malpighian corpuscle of a frog: *g*, glomerulus; *m*, the expanded invaginated end of a uriniferous tubule; *ut*, uriniferous tubule; *v*, *v*, blood vessels.

knot of vessels is very thin and it readily permits the diffusion of water and other substances from the blood into the cavity of the tubule.

It is mainly through the kidneys that the nitrogenous waste products are eliminated. The chief component of nitrogenous waste is urea (N_2H_4CO) which, it will be remembered, was the first organic compound fabricated by the chemist. The kidneys also eliminate several kinds of salts and other compounds, the water which passes through these organs serving largely as a vehicle for carrying away the dissolved waste material. Elimination in vertebrates is by no means exclusively carried out by the kidneys. The liver is an important excretory organ, which discharges various products of metabolism through the bile duct into the intestine. A certain amount of waste is also got rid of through the sweat glands of the skin. Most excretory organs are essentially tubular glands. Excretion is really a process of secretion, but it is distinguished by a separate term because the substances formed are of no use to the body.

The functions of absorption, assimilation, respiration, and excretion are but phases of the general activity of metabolism which constitutes the essential feature of life. Digestion is clearly a sort of accessory function, subsidiary to absorption; and circulation is another secondary function subsidiary to all of the others. Life as it evolves comes to require more and more machinery for its maintenance. And with the development of more machinery there comes the problem of making all the parts work together in a proper way so that the unity of the whole shall not be destroyed. This involves still more machinery, which is provided by the development of special mechanisms for coördination.

The great coördinating agency of the animal body is the nervous system, but most of the work of the nervous system is accomplished by means of muscles. Even in the Protozoa special muscular elements are distinguishable as myonemes, or contractile fibrils, and in nearly all the multicellular animals above the sponges there are well defined muscle cells. Muscles, which are

bundles of muscular fibers united by connective tissue, commonly occur in pairs, the contraction of the one member producing an effect which is opposite to that caused by the other. Flexors, which bend an appendage, are opposed by extensors, which straighten it; adductors, which draw a part toward the main axis, are opposed by abductors, which produce the reverse movement. Since muscles act by pulling and not by pushing, the utility of this prevalent arrangement is obvious. In the two layers of circular and longitudinal muscle in the body wall of the earthworm, we have an illustration of the same principle. The contraction of the longitudinal muscles obviously causes the body to shorten. The contraction of the circular muscles decreases the diameter of the body, and the cœlomic fluid, which is thereby subjected to pressure, naturally tends to force the body to increase in length. The locomotion of the earthworm, which involves the alternate lengthening and shortening of the body, is thus rendered possible through the opposed actions of the circular and longitudinal muscles of its body wall.

The larger part of the musculature of higher animals is attached to some kind of skeleton which serves not only as a protection and support to other parts of the body, but as a means of executing a great variety of movements. Skeletal structures are frequently found in very primitive animals, such as the Radiolaria and Foraminifera, mentioned in a previous chapter. Nearly all sponges possess a skeletal framework, consisting sometimes of carbonate of lime, sometimes of silica, as in the glass sponges, and sometimes of a horny substance as in the common bath sponge. In the corals there is a protective limy or horny skeleton secreted by the outer layer of the body, and in most molluscs there is an external coiled, or bivalved, shell, into which the body can be more or less completely withdrawn. Insects, crustaceans, and spiders have an external, segmented skeleton, formed, like the covering of the earthworm, by a chitinous secretion of the ectoderm. Chitin, when hardened through being impregnated with lime salts, forms a rigid external covering to which muscles are attached, which move the various parts. Owing to the

rigidity of their outer skeleton, continued growth in most of these animals is rendered possible only through shedding the skin. This is usually done several times during the growth of the animal.

In the vertebrates, most of the skeletal structures are internal. That very primitive relative of the vertebrates, Amphioxus, has, as a skeleton, an unsegmented gelatinous rod lying above the alimentary canal and just below the nerve cord. It is a significant fact that it is in the form of a notochord that the skeleton

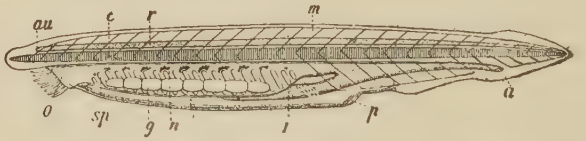

FIG. 73—*Amphioxus lanceolatus: a*, anus; *au*, eye spot; *c*, notochord; *g*, gonads; *l*, liver; *m*, muscles; *n*, nephridia; *o*, mouth; *p*, opening of the chamber surrounding the gills; *r*, dorsal nerve cord; *sp*, gill slits. (Diagram after Boveri.)

makes its first appearance in the embryonic development of all vertebrate animals. When we come to the primitive fishes, the sharks and their allies, we find a vertebral column consisting of a series of cartilages surrounding the spinal cord and connecting anteriorly with a cartilaginous skull which incloses the brain. The vertebral cartilages are formed around the notochord; they encroach more or less upon it in most fishes, and in the birds and mammals they practically obliterate it entirely.

The higher fishes have a well ossified skeleton, as do all the vertebrates above the fishes. There is a remarkable similarity in the general features of the skeleton in all vertebrates, from fishes to man. If we compare the skeleton of a codfish with that of a human being, we shall find in both a series of vertebræ inclosing the spinal cord and affording attachment to the muscles of the back and sides of the body; a skull composed, to a considerable extent, of corresponding bones; upper and lower jaws; a hyoid arch supporting the tongue, and two pairs of limbs attached to internal bony supports. Of course there are many differences in the two skeletons, as is inevitable in animals so dissimilar in other respects as a man and a codfish. For instance,

the codfish, being a gill breather, has a series of bony arches supporting the gills, but in man, who is a lung breather, these arches are almost entirely absent. But not quite, for a comparative study of the way in which the human larynx is formed shows that this structure contains parts of the old gill arches which have been worked in for a new use. There are important differences in the form of the limbs, although they are the same in number, namely, four. The fins of the codfish are supported by

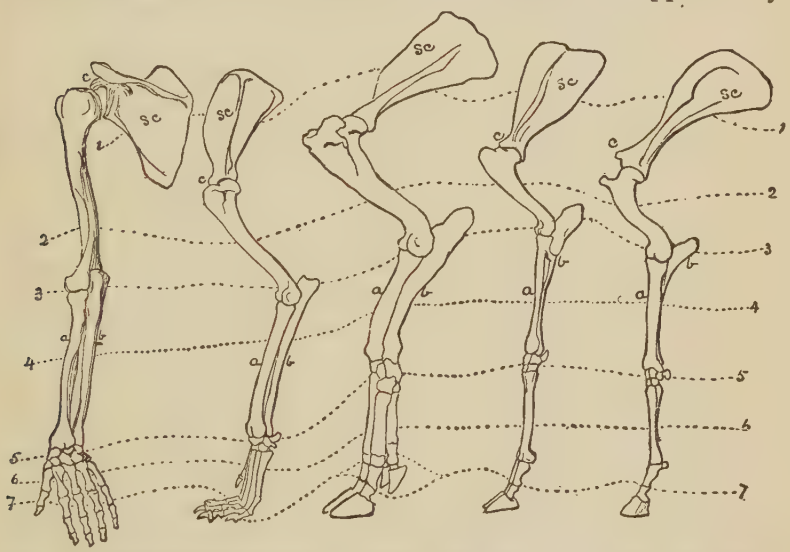

FIG. 74—Homologous bones of the four limbs of mammals. The dotted lines connect homologous parts. *1*, scapula; *2*, humerus; *3*, elbow joint; *4*, forearm; *5*, carpus; *6*, metacarpals; *7*, phalanges; *a*, radius; *b*, ulna; *c*, coracoid process of scapula, *sc*. (After Le Conte.)

many bony fin rays, whereas the limbs are of the pentadactyl, or five-fingered, type in man.

The fore fin of the fish and the arm of man are illustrations of what are called homologous organs, or organs of essentially the same plan of structure and relative position. Both of these organs are homologous with the wing of a bird or bat, the foreleg of a dog, and the flipper of a whale. The term analogous is applied to organs having a superficial similarity, or likeness of function, but no fundamental resemblance in their plan of struc-

ture. Illustrations of such are the wings of birds, which are modified fore limbs, and the wings of insects, which are formed by an extension of the chitinous covering of the body. There is no more attractive field for the study of homologies and the unity of plan which persists amid a great variety of modifications than that afforded by the skeletal structures of vertebrate animals. But as this is a general biology and not a comparative anatomy, we can do no more than indicate the existence of this field. We shall have something more to say on this topic, however, in a later chapter in connection with the theory of evolution.

Let us recur now to the nervous system, which as we have said is the great coördinating agency of the body. The primary and essential function of the nerve elements is to conduct impulses. If I dissect out the calf muscle of a frog's hind leg, leaving attached the nerve by which it is supplied, and then suspend the muscle in such a way that its contractions may readily be observed, I shall be able to make the muscle contract at will whenever I stimulate the end of its nerve. Something we call the nervous impulse travels along the fiber at a measurable rate, and this impulse is able to set up changes in the muscle which cause its fibers to shorten. Conduction is a fundamental property of living matter, which is simply emphasized in nervous tissue. We find it manifested in the protoplasm of the plant cell and in the unicellular animal. In fact, some of the Infusoria possess a system of fibrils which have been shown by microdissection methods to be probably specialized organs of conductivity.

The most primitive type of nervous system in the multicellular animals consists of scattered nerve cells and fibers connecting simple sense organs with muscle or gland cells. The nerve ring of the jellyfish marks an advance on this type, and in all forms higher than the Cœlenterates there is a concentration of nerve cells and fibers to form a central nervous system. A very common type is represented in the earthworm. There is a pair of closely united nervous masses, or ganglia, commonly called the brain, situated above the pharynx, near the anterior end of

the body. From the brain, cords pass around the pharynx, meeting on the ventral side in a paired ganglionic enlargement. From this there extends backward, along the ventral wall, a double nerve cord, having a pair of ganglia in each segment of the body. Nerves proceed from these ganglia to other organs situated in the same segment. Some of the fibers of these nerves extend from sense organs of the body wall to the ganglia where they branch and connect with other nervous elements. The nerves conducting impulses from sense organs to the ganglionic centers are called afferent, or sensory, fibers. There are other fibers

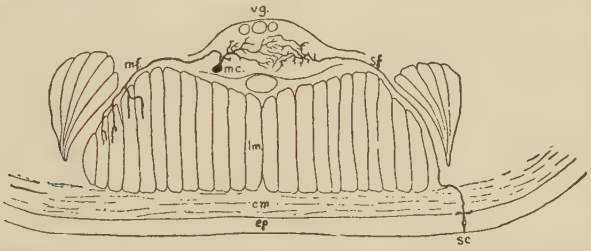

FIG. 75—Diagram of a cross section of the nerve cord and adjacent structures of an earthworm: *cm*, circular muscles; *ep*, epidermis, or outer layer of epithelium; *lm*, longitudinal muscles; *mc*, motor cell of nerve cord; *mf*, motor nerve fiber supplying the muscles; *sc*, sensory cell; *sf*, sensory nerve fiber; *vg*, ventral ganglion. (After Parker.)

originating in nerve cells within the ganglia and proceeding outward to terminate in gland cells or muscle cells. These are called efferent fibers, or in case they connect with muscles, they are known also as motor nerves. Within the ganglia many fibers cross from one member of the pair to the other, and other fibers pass anteriorly and posteriorly. There is thus formed a system of connections whereby a stimulus arising from any sense organ may be conveyed to almost any other part of the organism. If a worm turns away from an irritant applied to one side, the impulse proceeds from its stimulated sensory cells to a segmental ganglion, crosses over to its fellow, and then passes outward along a motor nerve to the longitudinal muscles of the opposite side of the body, which are thereby caused to contract and bend the body away from the stimulus. What the nervous system does in this case is to conduct impulses, and the particular way

FIG. 76—The central nervous system of an insect Machilis: *a*, nerve to antenna; *b*, brain; *e*, eye; *l*, labial nerve; *m*, mandibular nerve; *mx*, maxillary nerve; *o*, œsophagus; *ol*, optic lobe; *s*, subœsophageal ganglion; *sy*, sympathetic nerve; *I*, *II*, *III*, ganglia of the thorax; *1–10*, ganglia of the abdomen. (After Oudemans.)

in which the impulses are distributed depends upon the way in which the nervous elements are connected together in the central nerve cord. The ladderlike type of nervous system just described occurs in insects, crustaceans, arachnids, and related groups, but as a rule the brain is relatively larger and more complex than it is in the earthworm, and some of the segmental ganglia are commonly fused together.

When we come to the vertebrates, we find that the chief axis of the nervous system is dorsal to the alimentary canal, instead of ventral to it, and the whole structure of the spinal cord more compactly knit together than the ventral ganglia of the invertebrates. A segmental structure, however, is evinced by the fact that the pairs of nerves given off from the spinal cord correspond to the segments of the body. The spinal nerves arise by two roots, a dorsal, composed of sensory fibers, and a ventral, composed of motor fibers, but these two roots join before they emerge from the vertebral column in which the spinal cord is inclosed.

The spinal cord is the seat of many reflex acts, as may be shown in a frog whose brain has been destroyed or whose spinal cord has been severed near the head. If the hind foot of such a frog is stimulated, the leg will be flexed. In this reflex act the impulse aroused in the foot travels along a sensory nerve to the cord, and enters through a dorsal root into the central gray matter. There it is carried by means of one or more nerve cells, or neurons, to the motor nerve fibers, which pass out by the ventral root. Proceeding along the motor nerve, the impulse is distributed to the muscles of the leg, causing them to contract (Fig. 78).

In this reaction several neurons are involved, the impulse

being passed from one to another. Nevertheless, the response occurs with almost as great regularity, and perhaps as mechanically, as the contraction of an isolated muscle follows the stimulation of its nerve. There are spinal reflexes of various grades of complexity, and many of them are of great service in the life of the animal.

Fig. 77—Nervous system of man. (Courtesy P. Blackiston's Son & Co.)

The vertebrate brain is a very highly organized structure. It supplies several pairs of nerves to organs of the head, face, and other parts, and is the center for a number of important reflex acts. It receives the nerves from the more complex sense organs, such as those concerned with sight, hearing, taste, and smell. But its structure is largely given over to the higher kinds of nervous coördination and adjustment. This work is the special function of the cerebral hemispheres. These organs are not highly developed in lower vertebrates, but as we pass up the scale they become relatively much larger in size and more complex in structure. They are the seat of the higher mental functions, and it is not surprising that in man, who can be said, without undue boasting, to outstrip his mammalian relatives by far when it comes to intellectual pursuits, the cerebral hemispheres preponderate in bulk over all the rest of the brain.

An account, however cursory, of the structure and functions of the animal body, would be incomplete without some mention of the endocrine glands, or glands of internal secretion. Practically unknown only a few decades ago, internal secretions, or

hormones, as they are often called, are now in the limelight of the physiological stage. Instead of being emptied to the outside through a duct, internal secretions are discharged into the blood

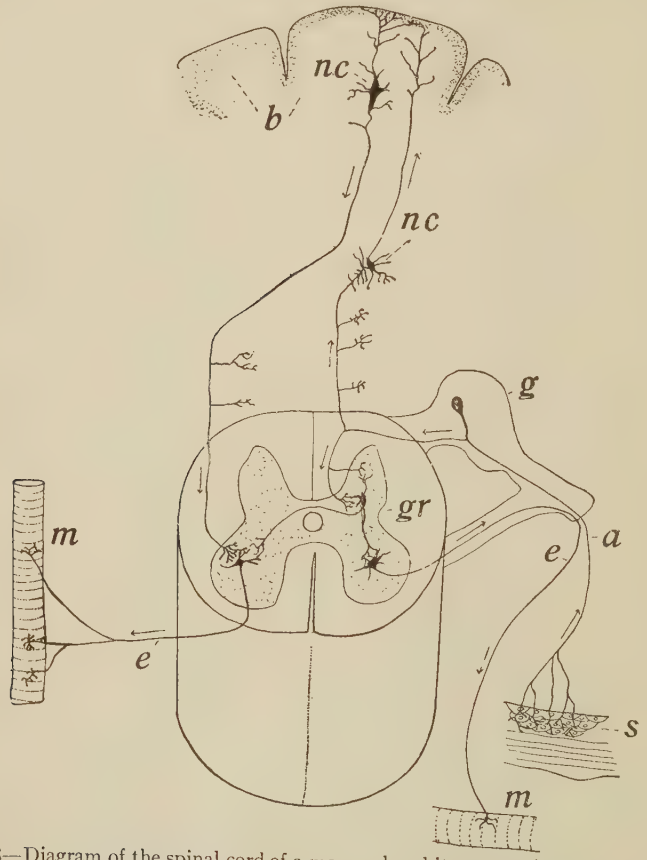

FIG. 78—Diagram of the spinal cord of a mammal and its connection with the brain: *a*, afferent, or sensory, nerve; *b*, part of brain; *e*, efferent, or motor, nerve fiber; *g*, spinal ganglion on dorsal root of a spinal nerve; *gr*, gray matter of spinal cord; *m*, *m*, muscle fibers; *nc*, nerve cell; *s*, sense organ. The arrows indicate the courses taken by the nervous impulses. (Modified from W. Mills.)

or lymph. So important are several of these internal secretions that the removal of the organs by which they are produced invariably results in death.

The idea of internal secretions, which was emphasized by

Claude Bernard in connection with his work on the glycogenic function of the liver, was brought into especial prominence by the experiments of Brown-Sequard. This versatile and somewhat eccentric investigator found that extracts of the testis injected into the blood appeared to exert a stimulating influence on the body. Later investigation has not altogether confirmed Sequard's conclusions, but it has been shown, without any doubt, that the testis forms an internal secretion, which profoundly influences many of the sexual characters by which males differ from females. As a result of practices long prevalent in certain oriental countries, it has been known for many centuries that, if the testes of male human beings are removed early in life, there is a scanty development of the beard, the voice remains high-pitched, and the general form of the body becomes more like that of a woman. Parallel phenomena are observed in the lower animals. Castration of young male deer prevents the development of horns, which normally characterize only the male sex. Steinach, who removed the testes of young male rats and grafted ovaries in their stead, found that these males failed to acquire the large size, rough hair, and pugnacious disposition that usually occur in male rats; on the contrary, the males exhibited a functional development of the mammary glands and the general behavior of the opposite sex. If testes are ingrafted in place of the ovaries in a female rat, she develops the larger size, rough hair, pugnacity, and sex instincts of the male.

These striking phenomena are readily explicable on the assumption that the sex glands produce substances which are given off into the blood and exert a specific influence on the development of certain bodily organs. The sex hormones not only modify physical development, but they profoundly affect instincts, disposition, and the character of the emotions. A feminized male rat will exhibit true, maternal solicitude toward the young of his species, and castrated roosters have been described as sitting upon eggs and brooding young chicks. Psychologically, the differences between males and females appear to be due mainly to the endocrine glands.

Among the organs of internal secretion absolutely essential in maintaining life are the adrenal, or suprarenal, glands. In man these bodies are situated just above the kidneys (Fig. 71 *s*). An English physician, Thomas Addison, while making post-mortem examinations of patients dying from a peculiar malady, since known as Addison's disease, which is characterized, among other symptoms, by a peculiar bronzing of the skin, observed that the adrenal glands presented a condition of structural degeneration. This discovery stimulated Brown-Sequard to ascertain the effect of removing the adrenals in a number of animals. He found that great weakness and spasms were produced, leading to death within one or two days. If one gland was allowed to remain, no unfavorable symptoms developed. Moreover, the life of the animal could be greatly prolonged by injecting an extract of adrenal glands into the blood. These glands apparently produce a secretion essential to life. Nowadays a substance has been extracted from them and is extensively used in medicine and surgery under the trade names of adrenalin and epinephrin. This substance has the property of constricting the walls of the arteries and hence causing an increase of blood pressure. It also puts new energy into a fatigued muscle, and it exercises a stimulating influence on the liver, causing it to give off more dextrose into the blood. Cannon has shown that under the influence of rage and fear an animal pours more of its adrenal secretion into the circulation, and is thereby better equipped for the activities of conflict or of flight. The active principle of the secretion has recently been obtained in a pure crystalline form and has been chemically analyzed. Chemists call it a dihydroxyphenyl-ethanol-methyl-amine and give it the formula $C_6H_3(OH)_2CHOHCH_2NHCH_3$, but if one is not a chemist, he may be excused if he does not remember it.

Another important endocrine gland is the thyroid, which is situated beneath the front part of the larynx. Like the adrenals it is a ductless gland. Histologically, it is composed of an aggregation of spherical vesicles, lined by a single layer of epithelial cells, surrounding a cavity containing a colloidal secretion. The

effect of removing the thyroid varies greatly with different animals, because there are other glands, the parathyroids, which may perform similar functions. Removal of both thyroids and parathyroids produces fatal results. The life of the animal may be preserved indefinitely, however, if an extract of the gland be injected into the blood, or even given per mouth in the form of tablets, which can now be purchased at any drug store.

The important internal secretion of the thyroid is a compound

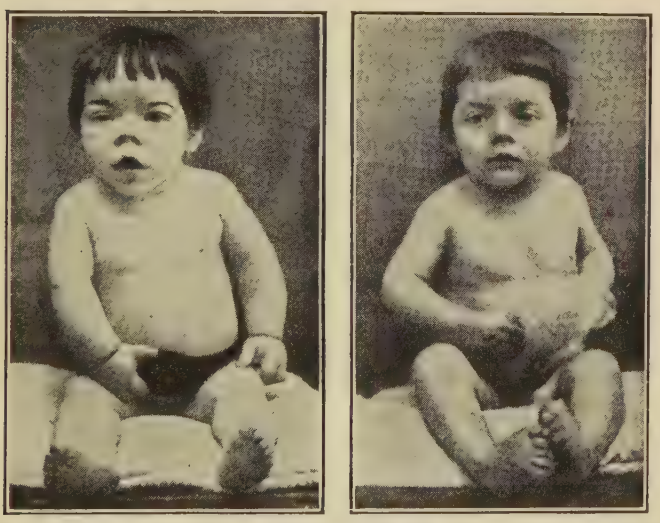

FIG. 79—Child with congenital cretinism. The left figure shows a condition of idiocy at two years and seven months of age. The right figure shows the same child five months later, after it had received treatments with thyroid extract. (After E. Suñer.)

containing iodine. A substance called thyroxin has been isolated in a pure crystalline state, which produces all the characteristic effects of the crude extract of the gland. Disorders of the thyroid are not uncommon, and are quite prevalent in certain localities whose natural waters are deficient in iodine compounds. It has been found that many of these troubles can be forestalled simply by giving a very minute amount of the iodides of potassium or of sodium with the food. Thyroid deficiency, when extreme, leads to a condition known as myxœdema, or

cretinism. Children afflicted with this malady may be born apparently normal, but as they grow older the skin becomes thick, coarse, and rough; the abdomen becomes large and swollen, the tongue enlarges, and often protrudes from the mouth; the hair becomes scanty; and the teeth develop in an irregular manner. There is a dulling of the mental faculties, leading often to a condition of pitiable idiocy. In some of the valleys of the Alps, cretins were at one time common, and cases of sporadic cretinism may develop in any locality. The plight of these unfortunate people was formerly hopeless, but since experimentation has revealed the functions of the thyroid gland, it has been found possible, by supplying the cretins with thyroid extract, to effect an almost complete cure. Many a repulsive idiotic cretin has been transformed into a comely, happy, and intelligent child through the administration of thyroid extract. But the treatment must be kept up, else the thick skin, the blank visage, and the stupor will recur, and intelligence will take its departure. The body, therefore, is dependent upon iodine. And so is the mind.

At the base of the brain, located in a little pocket in the skull, is a small organ about the size of a pea, known as the pituitary body. It is found in the same situation in all vertebrate animals, from the hagfish to man. From its great antiquity, it might be surmised that it probably has some important function, but its real use remained for a long time a complete enigma. It is formed in the embryo partly as an outgrowth from the brain, and partly as an outgrowth from the roof of the mouth, the two parts meeting and forming the two lobes, which can be recognized in the fully developed gland. These two lobes have different functions, which have not yet been completely disentangled. If the whole pituitary is removed death follows within a few days. Enlargement of the pituitary has been observed to result in gigantism, which is characterized by a curious enlargement of the bones of the face, hands, and feet.

It has been found that the pancreas, in addition to supplying several important digestive ferments, produces an internal

secretion of even greater importance. If the duct of the pancreas is tied, thus keeping the pancreatic juice from flowing into the intestine, the animal will remain alive, but removal of the whole organ quickly produces death. If, however, the organ, or only a part of it, is grafted in some other region of the body, the animal may continue to live. The hormone secreted by the pancreas has an important influence upon the metabolism of sugar. Removal of the pancreas produces a form of diabetes evinced by the appearance of abnormal quantities of sugar in the blood and urine. The cells responsible for the secretion of this hormone are probably those constituting the so-called islands of Langerhans, which lie outside the tubules which form the pancreatic juice. After ligation of the main duct, the cells of the pancreatic tubules atrophy, but those of the islands of Langerhans persist. It has often been observed that these islands exhibit degenerative changes in patients suffering from diabetes. Efforts to prepare an extract from the pancreas that could be successfully employed in cases of diabetes had long proved to be fruitless, until a few years ago when Drs. Banting and Macleod succeeded in extracting a substance called insulin, which when injected into the blood produces a marked reduction of diabetic symptoms. Diabetes apparently results from a defective condition of the islands of Langerhans, much as cretinism is caused by a defect of the thyroid gland, and it may be ameliorated in an analogous way by supplying the lacking hormone to the blood.

These endocrine glands produce a very slight amount of actual secretion. Aldrich finds that the addition to the blood of 0.000001 g. of adrenalin per kilo of body weight causes a marked rise of blood pressure. The total quantity of hormones in the blood at any one time is almost infinitesimal. Like the vitamines, which also occur in excessively minute amounts, they emphasize what Halliburton calls the rôle of the infinitely little in the processes of life. The hormones may be designated agents of chemical coördination, since they play a rôle in the integration of functions similar to that exercised by the nervous system. A single ex-

ample may suffice to illustrate this point. It has been known that when the acid contents of the stomach are liberated into the small intestine, the pancreas is stimulated to secrete pancreatic juice. Here is a typical illustration of the coördination, or working together, of different functions to achieve a particular result—the digestion of the food in the intestine. How is the coördination brought about? One might plausibly conjecture that it is effected through the agency of the nervous system, the stimulation of the walls of the intestine evoking a nervous reflex which excites the pancreas to secrete. Bayliss and Starling showed, however, that when all nervous connections between the intestine and pancreas had been cut, the pancreatic secretion nevertheless followed when an acid substance was present in the intestine. This is obviously inconsistent with the theory of a nervous reflex. The same investigators also showed that an extract from the mucous surface of the intestine would excite pancreatic secretion when injected into the blood. They drew the conclusion that the presence of acid in the intestine causes the production of a substance, which, diffusing into the blood and being carried to the pancreas, stimulates that organ to pour out its characteristic secretion. The hormone plays the part of a chemical messenger; and by virtue of its influence the pancreatic juice comes into the intestine just when it is most needed for the work of digestion.

The example of chemical correlation just cited is doubtless duplicated many times over in the integration of bodily activities. Through the agency of the endocrine glands and the nervous system, the manifold activities of the organs of the body are made to work together for the maintenance of the organic whole. These two systems of control have also a close interrelationship. They form what Berman, in his book *The Glands Regulating Personality*, has felicitously designated as the "interlocking directorate of the body." Much remains to be learned about the interrelations of these organs, but the field of inquiry is one which promises to throw much light upon problems not only of physiology, but of psychology as well.

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CHAPTER IX

EMBRYONIC DEVELOPMENT

Having given a brief account of some of the chief organ systems and functions of the animal body, we shall now consider the way in which the animal body comes to be formed. Each kind of animal, and plant also, has its own peculiar way of reaching its fully developed state. All higher animals begin their existence as a single cell called the ovum, or egg, which is produced in the ovary of the female. After being fertilized by the minute sperm cell of the male, the ovum proceeds to develop into an animal more or less like its parents. There is perhaps no phenomenon in organic nature more remarkable, or seemingly more miraculous, than the transformation of a single and apparently simple egg cell into the complex and wonderfully organized mechanism of the adult body. Development was formerly regarded by many biologists as due to the simple unfolding and growth of a preformed germ, the embryo being represented in miniature in the egg. Animals were conceived to develop much after the manner of the unfolding of a flower whose component parts are already present in the bud. Development was held to consist not in the formation of new parts, but in the growth of preëxisting rudiments. "No part in the animal body was formed before another," the great physiologist Haller declared; "all were created at the same time."

This view led to certain curious logical consequences which some of the extreme preformationists, such as Haller and Bonnet, did not hesitate to accept. If the egg contains the adult form in miniature, it must therefore contain other eggs, which in turn contain still others, and so on until all possible progeny are provided for. This is the so-called box-within-box theory. Some of the expounders of this doctrine calculated that there must

have been 200,000 millions of germs in the ovary of Eve in order to account for her existing descendants. The discovery of the spermatozoön and the part it played in causing the egg to develop, gave rise to the question whether the preformed germ was contained in the sperm or the egg. Naturalists became divided into two rival camps, the ovists and the animalculists, the former contending that the embryo is contained in the egg, the latter that it is contained in the sperm. Some of the animalculists who supplemented their rather imperfect microscopes with a particularly lively imagination, actually figured the head, arms, and legs of a man in the head of a spermatozoön!

Fig. 80—A human spermatozoön: *h*, head; *m*, middle piece; *t*, tail. (After Retzius.)

Sharply opposed to these preformation theories was the doctrine of epigenesis, championed in 1759 by Caspar Friedrich Wolff in his celebrated *Theoria Generationis*. Wolff was a diligent student of the development of the chick, and he maintained that at the beginning of development the germ consists merely of simple, unorganized matter which, in consequence of fertilization, gradually takes on a more complex and highly organized form. After the cell theory came to be established in 1838–39, it was soon recognized that the egg is a single cell, and later studies demonstrated that the spermatozoön is also a single cell. The older theories of preformation were definitely set aside, and a much clearer insight was gained into the true nature of embryonic development. It is a remarkable fact that it was only in a relatively recent period that organisms were clearly shown to develop at all. Even after the beginning of the nineteenth century it was still possible for the preformationists to maintain that development is merely an appearance due to our imperfect means of observing the initial stages in the growth of the embryo.

Commonly embryonic development is said to begin with the fertilization of the egg by the sperm cell. Before describing this process, however, it is desirable to give an account of the germ cells and the changes which they undergo preparatory

to their union. The eggs, or ova, are formed in most animals within special organs called ovaries. They arise from the primordial germ cells, which are much the same in both sexes. After dividing many times, as the body grows and develops, the primitive egg cells, or oögonia, finally enter upon a period of growth. The female germ cell, at this stage, is known as an oöcyte, and when its growth period is completed, it is discharged from the ovary and passes, generally through an oviduct, to the outside. The growth of the oöcyte or, as we may now call it, the unfertilized egg is mainly due to the accumulation of yolk, which serves as a sort of food supply for the developing embryo. In the birds the original egg cell, which corresponds to what we call the yolk of the egg, becomes surrounded by other materials during its passage down the oviduct. First it receives a coating of albumen, the white of the egg, secreted by the glands of the oviduct, and then there is secreted around the whole the calcareous coating which forms the shell. The egg of a bird consists, therefore, of the ovum proper, plus the surrounding coatings of nutrient and protective materials, with which all eaters of eggs are familiar.

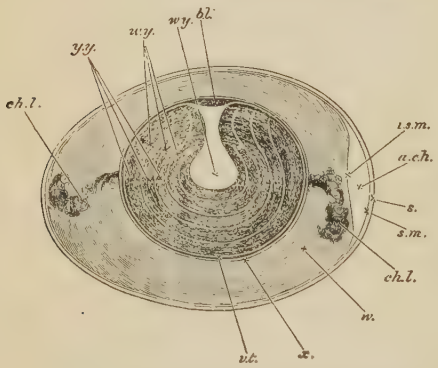

FIG. 81—Section through a hen's egg. *ach*, air chamber; *bl*, blastoderm; *chl*, chalaza, the suspensory of the yolk; *ism*, internal shell membrane; *s*, shell; *sm*, external shell membrane; *vt*, vitelline membrane; *w*, white or albumen; *wy*, white yolk; *x*, layer of fluid albumen; *yy*, yellow yolk. (From Balfour.)

In a great many animals, the eggs have no protective envelopes. In numerous aquatic forms the eggs are discharged into the water to take their chances of destruction or successful development. Among all the mammals, with the exception of the most primitive order of egg-laying monotremes, the eggs, which are very small, develop within the body of the parent. Such forms are called viviparous, a word which means bearing living young,

the egg-laying forms, like the birds, being called oviparous (literally, bringing forth eggs).

One very important event in the preparation of the egg for beginning its career of development remains to be described. This is the process of maturation, a process which consists essentially in the reduction of the number of its chromosomes to one-half the number found in the cells of the body or the primordial germ cells. It should be borne in mind, when considering the phenomena of maturation, that the chromosomes of all animals developing from fertilized eggs are partly maternal and partly paternal in origin. This is due to the fact that in fertilization the sperm cell brings into the egg a number of chromosomes, which is usually equal to the number of egg chromosomes. Sexually reproduced organisms are, as it were, dual creatures in respect to their chromosome equipment. As we shall see later, this is a very significant fact in relation to heredity, since organisms inherit their qualities to about the same extent from both of their parents. During the series of cell divisions that take place in the life of the individual, the chromosomes of both sex and body cells divide longitudinally by the typical process of mitosis and retain their number throughout. At a certain period in the history of the sex cells, however, the usual method of division is superseded by the process of reduction, which is apparently anticipatory to the doubling of the chromosome number that occurs in fertilization. Were it not for this reduction, the chromosome number would be doubled in each generation, and this in time would lead to serious complications. By the preliminary halving of the chromosome number in the germ cells of both sexes, and the restoration of the complete number that is effected when the egg is fertilized, the chromosome complex characteristic of a given species is kept constant through successive generations.

Just previous to the divisions by which the chromosomes of the sex cells are reduced in number, there occurs a temporary pairing of chromosomes which is known as synapsis. Little was known of this process until a few years ago, but what has now been dis-

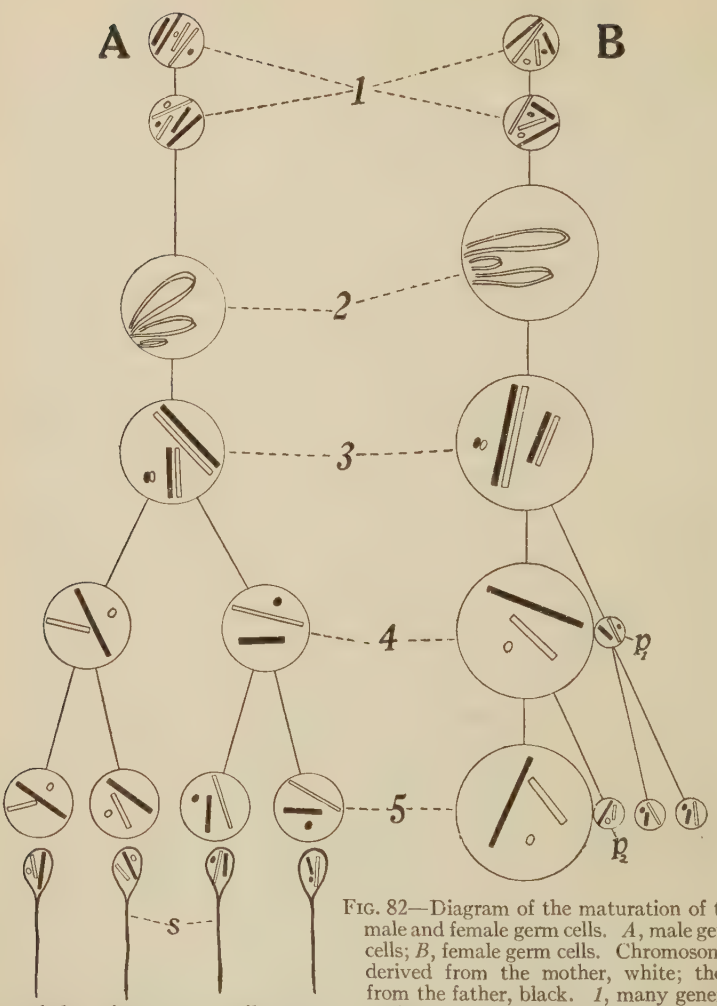

FIG. 82—Diagram of the maturation of the male and female germ cells. *A*, male germ cells; *B*, female germ cells. Chromosomes derived from the mother, white; those from the father, black. *1*, many generations of the primary germ cells, spermatogonia and oögonia, in which each of the six chromosomes divides longitudinally. *2*, period of synapsis in which the germ cells of both sexes, especially those of the female, increase in size. In this stage the chromosomes consist of long, paired threads. *3*, a later stage of synapsis in which the chromosomes are shorter and thicker. In each pair one chromosome is maternal and one paternal in origin. *4*, first maturation division, resulting in the separation of the members of each pair of chromosomes—a true reducing division. In the male this division is equal; in the female it is very unequal and results in the formation of a small polar body, p_1. *5*, second maturation division, in which each chromosome divides longitudinally—a non-reducing division. In the female this results in the formation of the second polar body, p_2. *s*, spermatozoa into which each of the male sex cells indicated in *5*, is transformed.

covered concerning it has thrown much light on the significance of maturation and the probable mechanism of heredity. The process of reduction is preceded by a growth period, in which there is a relatively slight growth in the primordial sex cells of the male, and a much more extensive growth, as a result of the accumulation of yolk, in the sex cells of the female. The chromosomes in the period of synapsis appear in the form of long threads, which lie side by side in pairs. The threads draw more closely together, apparently fusing for a time, and then separate in preparation for the next cell division. There is evidence that this pairing of chromosomes is not haphazard, but that one member of each pair is maternal and the other paternal in origin. Some of the evidence for this conclusion is derived from the behavior of characters in inheritance, but there is also very cogent evidence derived from direct cytological observation. In many organisms the chromosomes are similar in size and shape, so that the cytologist cannot distinguish one from another, and often he has difficulty enough in seeing them at all. In other cases, fortunately, the chromosomes are relatively large, few in number, and present differences in size and shape which make possible their identification. The large, lubber grasshopper, studied by Sutton, proved to be especially favorable for such investigation in having nice, large chromosomes of a varied assortment of sizes. Moreover, there were found to be two chromosomes of each of the various sizes, one presumably maternal in origin and the other paternal. The reduced germ cell contains only one member of each given size. In other words, the germ cells contain one set of the different sizes of chromosomes, whereas the body cells contain a double set. Now in the period of synapsis, the pairs of chromosomes were observed to be made up of members of approximately the same size and shape, and the only conclusion to be drawn from this fact appears to be that each chromosome of male origin pairs with a corresponding chromosome of female origin. How they find their predestined mates we do not know. Up to the period of synapsis the chromosomes of male and female origin go on dividing in

seeming independence and indifference, but synapsis ushers in an epidemic of mating. It is the period of the marriage of the chromosomes; each selects its elective affinity. But the marriage is of short duration, being speedily followed by divorce.

The separation of the pairs takes place during the two cell divisions which follow synapsis. Only one of these divisions, commonly the first, is a true reducing division, or one which reduces the chromosomes to one-half of their previous number. The other division is of the usual, or equational type, which is due to the longitudinal splitting of each single chromosome. With the completion of these two divisions, the maturation of the sex cells is accomplished.

It frequently happens that in the maturation divisions, which commonly follow in close succession, each chromosome divides before the previous cell division is completed. Hence, the chromosomes may appear in groups of four, called tetrads. One division involved in tetrad formation consists in separating two chromosomes which had previously paired in synapsis—a true reducing division—the other consisting in a division of each of these separated chromosomes. During the two cell divisions occurring in maturation, the four components of the tetrads become separated so that each component lies in a separate cell.

So far as the behavior of chromosomes in synapsis and maturation is concerned, the germ cells of both sexes have practically the same history. The enormous differences in size and shape which characterize the mature germ cells of the two sexes are obviously related to the very different functions which these cells perform. The cell divisions which effect reduction in the egg are very unequal, and result in the formation of two minute cells called polar bodies. Both polar bodies disintegrate without taking any part in development. Each polar body, as it is formed, receives the same number of chromosomes that is retained in the egg, together with a minimal amount of cytoplasm. This very unequal division of the cytoplasm is a sort of device to retain in the egg the relatively large amount of nutrient material that was stored during its growth.

In the maturation divisions of the sperm cells, on the other hand, the cytoplasm is divided into approximately equal parts, the two divisions following synapsis resulting in the formation of four smaller cells which are transformed into spermatozoa. A typical spermatozoön consists of a head, which is mainly formed of the closely packed chromosomes of the nucleus; an elongated motile tail, by means of which it swims actively about; and a

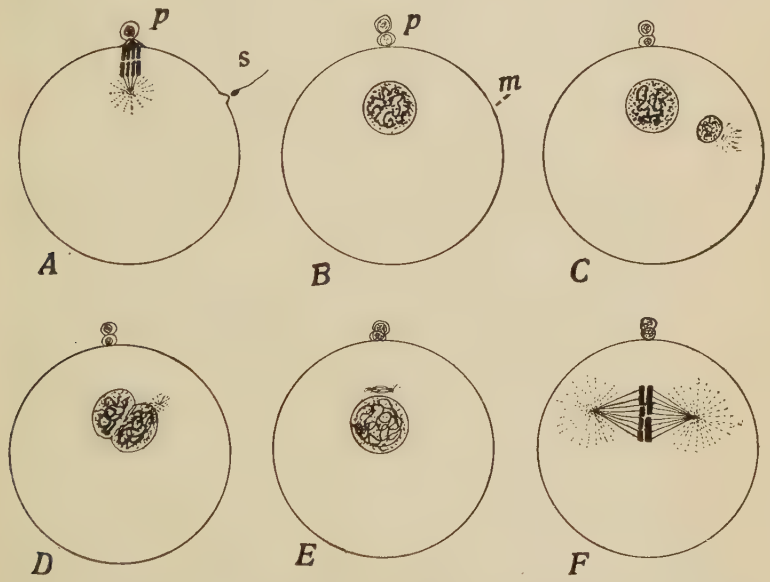

FIG. 83—Diagram of the fertilization of the egg: *A*, egg having given off one polar body and in process of giving off the second one. A sperm cell, *s*, is about to enter the egg at the point indicated by the attraction cone. *B*, both polar bodies formed and the nucleus of the egg in a resting condition, the male sperm head forming the male pronucleus, *m*, near the periphery. *C*, male pronucleus enlarged and approaching the female pronucleus. *D*, meeting of the two pronuclei. *E*, the two pronuclei fuse into one; the male center has divided to form the centers of a small spindle. *F*, first cleavage of the egg; *p*, polar bodies.

minute middle piece, near the base of the tail, which is in part derived from the centrosome (Fig. 80). In the formation of the spermatozoön, most of the cytoplasm of the male sex cell goes into the tail, and all of the nucleus goes into the head.

The function of the spermatozoön is to find and fertilize the egg. While we speak of the spermatozoön as a cell, it is really a

little organism complete in itself, endowed with independent activity and capable of responding to various stimuli. In many species, its function of fertilizing the egg is facilitated by the circumstance that the egg gives off a substance to which the sperms are attracted. In other cases, the sperms not improbably collide with the egg simply by accident, but when a sperm cell comes in contact with the egg, it proceeds to penetrate the egg substance. As a rule only the head and middle piece of the sperm enter, the tail being left at the periphery. The head now

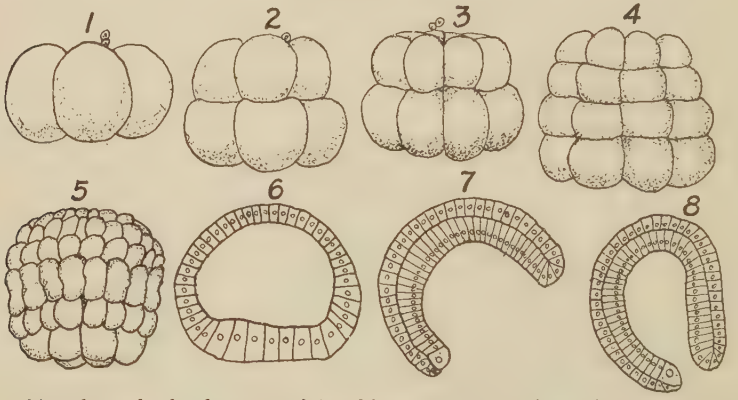

FIG. 84—The early development of Amphioxus: *1*, *2*, *3*, *4*, four, eight, sixteen and thirty-two cell stages respectively; *5*, blastula seen from the outside; *6*, section through blastula; *7*, beginning gastrula stage; *8*, later gastrula stage. (After Hatschek.)

enlarges and assumes a spherical form, becoming the so-called male pronucleus. It approaches the nucleus of the egg, or female pronucleus, with which it eventually fuses, thus forming the nucleus of the fertilized ovum, which is thus, as we have previously observed, partly of maternal and partly of paternal origin.

Eggs frequently exhibit a curious reaction which prevents them from being entered by more than one sperm. The first sperm cell that succeeds in penetrating into the egg cytoplasm stimulates it to undergo a change at the surface, which prevents other sperms from gaining entrance. Were it not for this delicate and rapid reaction, eggs might be fertilized by several sperm cells.

When this occurs, as it does under exceptional circumstances, it frequently leads to abnormalities of development.

The act of fertilization, in addition to bringing to the developing organism the hereditary contributions of its two parents, affords a stimulus which causes the egg to divide. In typical cases this process of cleavage divides the ovum successively into two, four, eight, sixteen, etc., cells. As cleavage goes on, there is formed a solid group of cells called the morula; then the blastula,

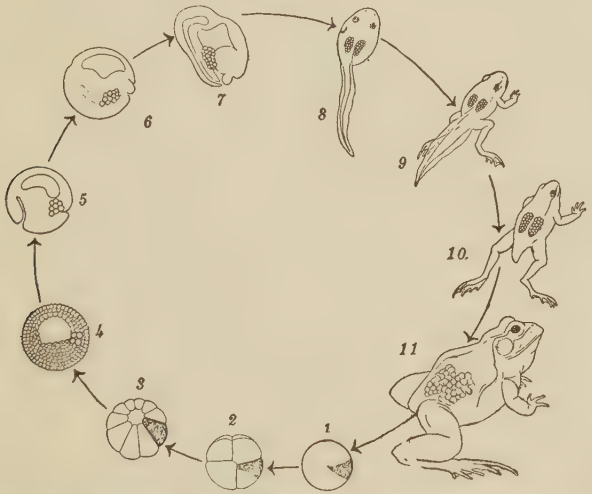

FIG. 85—Diagram of the life cycle of the frog: *1*, fertilized egg—the darkened area is the part which gives rise to the cytoplasm of the germ cell; *2*, eight-cell stage; *3*, thirty-two-cell stage; *4*, blastula showing germ cells in heavier outline; *5-7*, successive stages in the development of the gastrula, showing the germ cells; *8-10*, transformation of the tadpole into the frog; *11*, mature frog with eggs in ovaries ready to be discharged. (After Conklin.)

or hollow ball stage, is formed by the appearance of a cavity in the center of the mass; then there follows the gastrula stage, in which one side of the blastula wall becomes pushed in, much as one might push in one side of a hollow rubber ball. The gastrula is a sort of double-walled cup, the outer layer of which is now called the ectoderm, and the inner the entoderm. The open mouth of the gastrula, which is called the blastopore, becomes reduced in size, and in many animals completely closes.

The eggs of animals, in general, exhibit a characteristic called

polarity. At one end, called the animal pole of the egg, the protoplasm is more concentrated than elsewhere, and the nucleus lies nearer this part of the egg than it does to the opposite, or vegetal pole. As a rule cleavage proceeds more rapidly near the animal pole, and hence the cells are usually smaller in this region than those of the vegetal pole of the egg, where there is

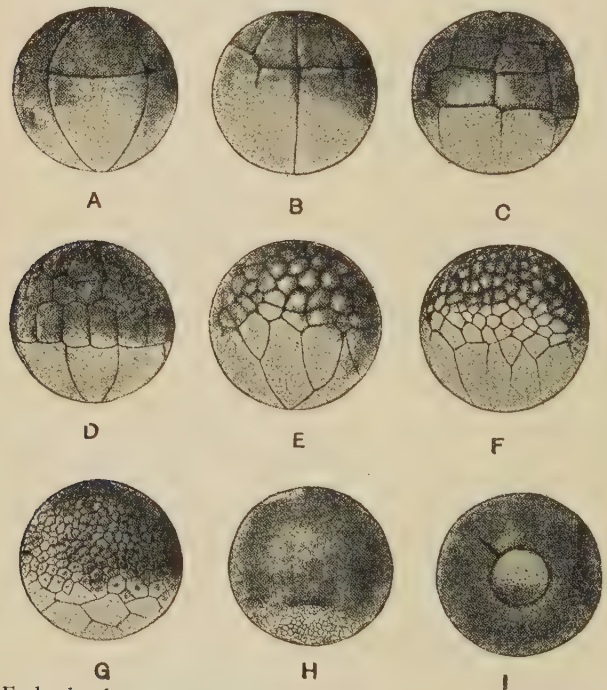

FIG. 86—Early development of the frog's egg: *A*, eight-cell stage; *B*, sixteen-cell stage; *C*, thirty-two-cell stage; *D*, *E*, *F*, *G*, successive stages showing the more rapid division of cells near the dark animal pole of the egg; *H*, beginning gastrula; *I*, later gastrula. (After Morgan. Courtesy Macmillan Co.)

more yolk. It is the cells of the vegetal pole that become pushed in to form the entoderm, so that the polar axis of the undivided egg bears a quite definite relation to the main axis of the gastrula and later stages of development.

The way in which development is carried on varies greatly in different forms. The stages just described represent typical

steps which are passed through in the development of most of the multicellular animals. To follow the further steps of the process, it will be desirable to confine our attention mainly to a particular form, such as the frog, which serves very well as a type of vertebrate development in general. The frog's egg is pigmented above and light-colored at the vegetal pole, and it divides, in accordance with the general scheme we have outlined, to form a morula, blastula, and gastrula stage, although the latter is pro-

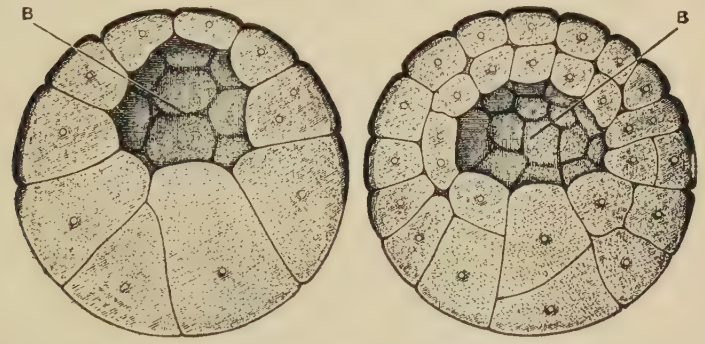

FIG. 87—Sections through the frog's egg in the blastula stage showing the central cavity, *B*. (After Marshall.)

duced partly by invagination (or inpushing), and partly by the ectoderm overgrowing the entoderm. The pigmented ectoderm cells, which are derived from the dark, upper, or animal pole of the egg, gradually extend downward and finally completely close over the blastopore. Before gastrulation is completed, a third germ layer, the mesoderm, makes its appearance between the ectoderm and entoderm. It arises from near the edge of the blastopore and pushes its way between the other germ layers. As the blastopore closes mainly from in front backward, the mesoderm appears as two sheets brought near each other in the mid-dorsal line. Finally, the ventral or lower edges of the mesoderm meet and fuse on the ventral side, thereby separating completely the entoderm from the ectoderm. A split appearing in the mesoderm of each side separates it into two layers, one of which becomes applied to the entoderm, the other to the ec-

toderm, the space between them forming the cœlom, or body cavity.

Even before the blastopore is completely closed, there appear dorsal thickenings, or folds, of the ectoderm, extending along what is to be the long axis of the embryo. These are the medullary folds, and the depression between them is the medullary groove. The groove sinks in and the folds grow over it on either side and finally meet and fuse above, converting it into a tube. This tube, which later becomes completely separated from the

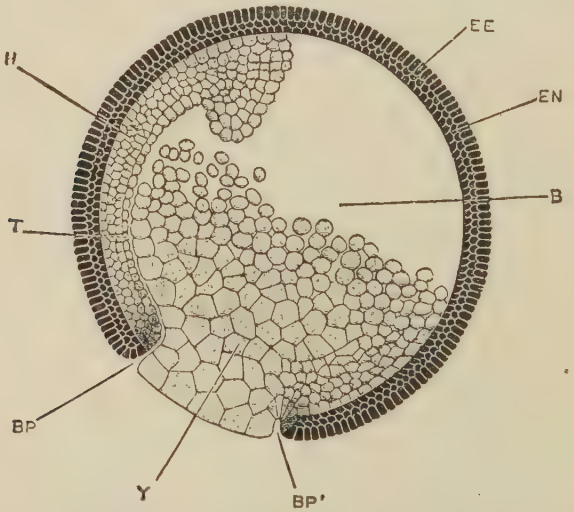

FIG. 88—Longitudinal section through a frog's egg in the gastrula stage: *B*, blastula cavity; *BP*, *BP'*, edges of the blastopore; *EE*, outer, and *EN*, inner layer of ectoderm; *H*, hypoblast, or entoderm; *T*, cells of beginning notochord; *Y*, yolk-laden cells of entoderm. (After Marshall.)

superficial ectoderm, forms the beginning of the nervous system. Its anterior end enlarges and gives rise to the brain, the remaining part becoming the spinal cord. At a later period nerves bud out from both brain and cord and extend through the other tissues and make connections with the muscles, sense organs, and other parts of the body (Figs. 90 and 91).

After the blastopore closes, the embryo begins to elongate. A strand of cells just above the dorsal side of the primitive

gastrula cavity, or archenteron, and just below the medullary tube, becomes separated off from the entoderm below and the mesodermic layers on either side. This strand develops into a rodlike body, the notochord, which forms the beginning of the vertebral, or spinal column. Later, the notochord, as in higher vertebrates in general, becomes almost completely obliterated by the bony vertebræ which develop around it from the surrounding mesoderm.

The entoderm gives rise to the inner lining of the alimentary

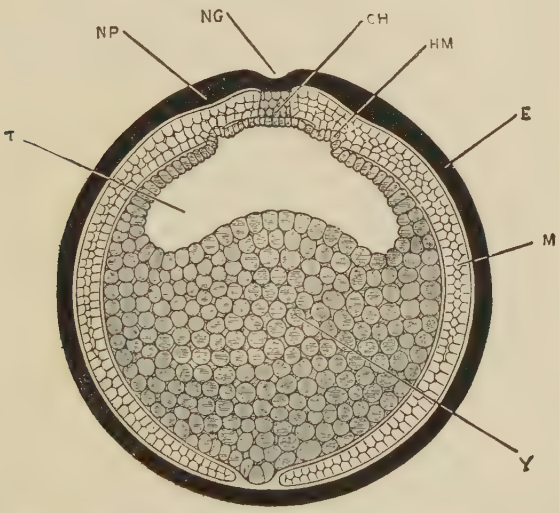

FIG. 89—Cross-section of frog's egg in late gastrula stage: *CH*, notochord; *E*, ectoderm; *M*, mesoderm; *NG*, neural, or medullary, groove; *NP*, beginning of neural folds; *T*, archenteron, or cavity of the gastrula; *Y*, yolk-laden cells of entoderm. (After Marshall.)

canal and all the organs which arise as outgrowths from it. One of these is the liver, which begins as an outpushing of the ventral side near the anterior end. This outpocketing branches repeatedly, forming the highly complex cluster of tubules of which the adult liver mainly consists. The connective tissue, blood vessels, and outer covering of the liver, are derived from the mesoderm. Another outpocketing of the primitive alimentary canal forms the beginning of the pancreas.

With the elongation of the body, the inner cavity, which constitutes the alimentary canal, becomes drawn out into the form of a tube. When the blastopore closes, the alimentary canal is temporarily cut off from communication with the outside, but at a later period an inpushing from the ventral side of the anterior

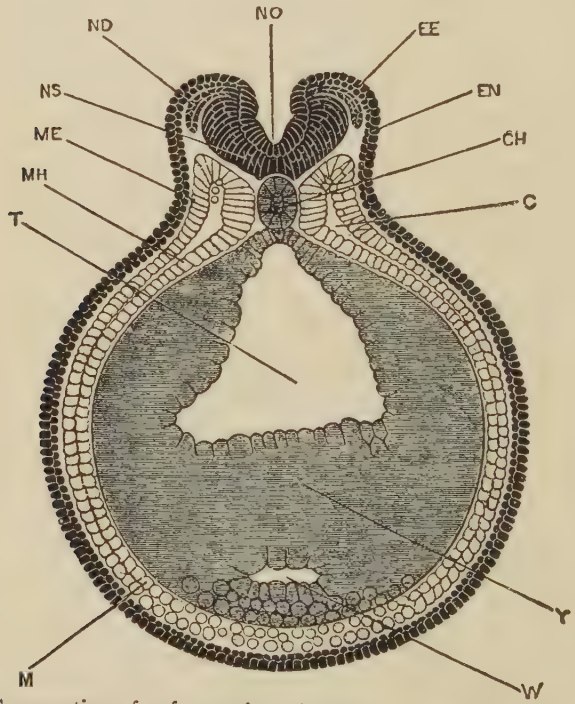

FIG. 90—Cross-section of a frog embryo before the closure of the neural folds: *C*, cœlom; *CH*, notochord; *EE*, epidermic layer of ectoderm; *EN*, inner, or nervous, layer of ectoderm; *M*, mesoderm; *ME*, outer layer of mesoderm; *MH*, inner layer of mesoderm; *NO*, neural groove; *ND*, dorsal root of spinal nerve; *NS*, beginnings of spinal cord; *T*, archenteron; *W*, cavity of liver; *Y*, yolk. (After Marshall.)

end of the embryo occurs, which meets with the entoderm, and then the walls separating the two cavities break through thus forming an opening between the outside and the primitive digestive cavity. This inpushing from the outside, which is known as the stomodeum, forms the lining of the mouth cavity, which is therefore ectodermic in derivation. A similar inpushing,

the proctodæum, meets and breaks through into the posterior part of the alimentary canal, thus completing a continuous passageway from the mouth to the outside near the opposite end of the body.

From the ventral side of the alimentary canal, just behind the

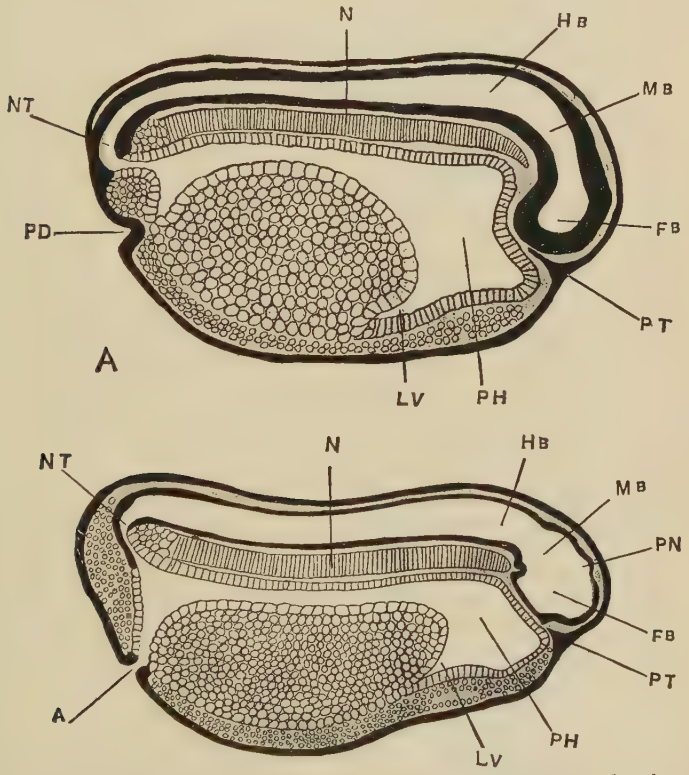

FIG. 91—Longitudinal sections through young frog embryos after the closure of the blastopore. Upper figure shows beginning of procotodæum, or anal invagination. Lower figure shows the fusion of this invagination with the archenteron. *A*, anus; *FB*, fore brain; *HB*, hind brain; *LV*, beginning of liver; *MB*, mid-brain; *N*, notochord; *NT*, temporary passage between the nerve tube and archenteron; *PD*, proctodæum; *PH*, archenteron; *PN*, pineal gland; *PT*, ingrowth to form the pituitary body. (From Morgan, after Marshall.)

mouth cavity, there is pushed out a bilobed outpocketing, which develops into the lungs. Near the posterior end of the ventral side of the alimentary canal there is another outpocket-

ing, which forms the urinary bladder. The inner lining of all these organs which arise as outgrowths of the alimentary canal, is formed of entoderm, but their muscular and connective tissue investments are formed from the inner layer of the mesoderm, which we have mentioned as becoming applied to the alimentary canal.

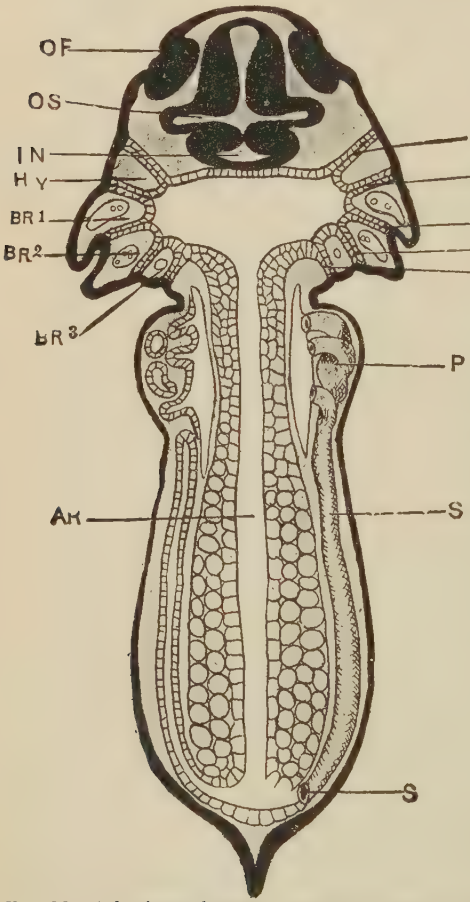

FIG. 92—A horizontal section through a frog embryo: *AR*, archenteron; BR^1, BR^2, BR^3, gill arches; H^1, H^2, H^3, gill slits; *HB*, hyoid cleft; *HM*, hyomandibular cleft; *HY*, hyoid arch; *IN*, infundibulum; *OF*, olfactory pit; *OS*, stalk of optic nerve; *P*, tubules of the pronephros or primitive kidney; *S*, segmental duct. (From Morgan, after Marshall.)

A little after the rudiments of the preceding organs develop, there appear five pairs of vertical pockets on either side of the wall of the pharynx, or posterior part of the mouth cavity. These meet and fuse with the ectoderm, which breaks through at the points of contact, so as to form a double series of openings between the pharnyx and the outside of the body. These openings are the gill slits, and their margins are thrown into folds which constitute the internal gills. Between the slits the ectoderm of the neck region produces the branched external gills, which are conspicuous in the early free stages of the tadpole. The tadpole breathes like a fish, taking

water into the mouth and passing it out through the gill slits, where it comes into contact with the filaments of the gills.

The mesoderm, whose devlopment we have traced to a stage in which it is composed of two layers separated by the cœlom, gives origin to a large part of the organs and tissues of the body. The layer that becomes applied to the entoderm forms the muscular and connective tissue parts of the alimentary canal, and its various derivatives; the outer layer constitutes the inner layers of the skin and the musculature of the body wall. The mesoderm also forms most of the other muscles, the skeleton, heart and blood vessels, kidneys, organs of reproduction, and many minor parts. The ectoderm gives rise to the outer, or epithelial layer of the skin, the nervous system, the lining of the cavities of the mouth and nose, the retina, lens, and cornea of the eye, and the sensory epithelium of the inner ear.

When we consider the way in which the primary rudiments of the organ systems of the body are formed, we see that it is usually by a process of folding, outpushing, or inpushing of the germ layers. Not only is the original entoderm formed by invagination, but its chief derivatives—lungs, gill slits, liver, pancreas, and bladder—arise by a somewhat similar process. So also do the smaller glands which occur in the stomach and intestine. The nervous system begins as an infolding, and the nasal cavity and auditory pits form in a similar way. And were we to trace the formation of the organs that arise from the mesoderm, we should find further illustrations of the same method.

As the embryo develops, the parts become more and more unlike each other. Their component cells, at first of much the same primitive type, differentiate along diverging lines, some becoming specialized muscle cells, others nerve cells, others connective tissue corpuscles, and so on. Histogenesis, or tissue differentiation, goes along with the development of organs; and accompanying this differentiation of structure, there is a parallel differentiation of function. The parts of an embryo finally come to perform many different activities, but the growing diversity of embryonic organs is one which is subordinated to the unity

of the organism. The parts work together at all stages of the process to maintain the harmonious coördinated development of the whole. How and why the diverse parts are coördinated in their ever changing relations is one of the unsolved problems of biology. As we have stated in the beginning of the chapter, the wonder of development is one of the most striking of all the wonders which living beings exhibit.

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CHAPTER X

THE PERPETUATION OF LIFE

A large part of the business of living is concerned with the production of the next generation. Life is always bent on its own perpetuation, and the process of reproduction is only one of its many devices for cheating death. If the grim reaper overtakes the individual, as he always does in the higher organisms, life wins in the game through the production of new individuals from the bodies of the older ones before they die. The perpetuation of kind is a problem which organisms solve in ways which are almost as numerous and varied as the activities of the organisms themselves. Some of these ways are very simple, others are very elaborate and ingenious. Obviously we can consider only a few of them in the present chapter.

One of the simplest modes of perpetuating life is ordinary binary fission, by which the organism is divided into two similar parts. This is the prevalent fashion of reproduction among the bacteria, the unicellular algæ, and most groups of the Protozoa. A variation of this method occurs in reproduction by budding, which is a sort of unequal fission. Even very low organisms, such as the yeast plants, reproduce by budding, and the method occurs more or less in many other one-celled forms. It is a notoriously common method of propagation among plants. It is common among sponges, and in the hydroids and coral polyps. In the fresh-water Hydra which usually propagates in this way, the buds which protrude from the sides of the body contain both ectoderm and entoderm and a central cavity which connects with the general digestive cavity of the parental organism (Fig. 52). Tentacles push out around the distal end of the bud, a mouth forms between them, and the bud finally constricts off at the base, and becomes an independent Hydra. In the hydroids the

buds usually remain attached to the stem and they may form a much-branched colony, simulating the form of a higher plant, which is developed by a somewhat similar method. A number of worms bud off small incipient individuals at the posterior end of their bodies. The tunicates, coral polyps, and several other kinds of attached, or sessile, animals may form colonies of numerous individuals by a continued process of budding.

What is called spore formation is another variation of fission. In one-celled organisms there is frequently a series of nuclear divisions without an accompanying division of the cytoplasm, after which the cytoplasm aggregates around each nucleus, and the whole breaks up into a number of small, nucleated masses called spores. This is the method of reproduction among the Sporozoa, and it is found also in other Protozoa, and in some of the unicellular plants.

All of the preceding modes of perpetuating the species are examples of asexual reproduction. In sexual reproduction there is a union of gametes, or sexual cells, which precedes, and is often necessary to initiate, the reproductive process. As we have already seen, sexual reproduction occurs in both unicellular and multicellular organisms. It is not quite coextensive with life, because, so far as we know, it is not found in the very simplest of the one-celled organisms, the bacteria and the blue-green algæ. It has also never been discovered in several groups of flagellates. Scientific caution should prevent our asserting positively that sexual reproduction does not occur among these minute forms, and in fact, some investigators hold that there is evidence for its existence even in the bacteria. Any day some assiduous observer may prove that it occurs. Nevertheless, there has been much careful search for indubitable proof of its existence, but thus far in vain.

The simplest manifestation of sexual reproduction is the conjugation of unicellular organisms. This commonly occurs after a series of generations produced by the ordinary process of fission. In Hæmatococcus it has been found that the free-swimming flagellated cells meet and fuse in pairs, literally becoming one

flesh, the two nuclei, as well as the cytoplasmic bodies, becoming united into one (Fig. 29). There is here no marked difference between individuals of the fusing pairs, so that we cannot speak of either member as male or female. There are other unicellular forms where one individual, the female gamete, is relatively large and passive, while the other, the male gamete, is much smaller and

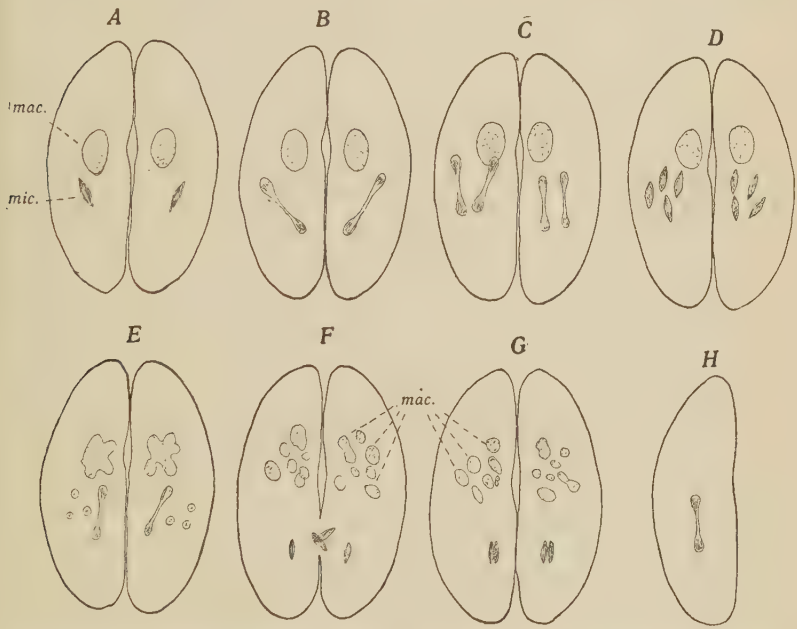

FIG. 93—Conjugation in Paramœcium: *A*, two Paramœcia with their oral surfaces in contact; *mac*, macronucleus; *mic*, micronucleus. *B*, division of each micronucleus. *C*, each of the two micronuclei resulting from the preceding division again dividing. *D*, stage with four micronuclei in each Paramœcium. *E*, three of the micronuclei degenerating, the fourth dividing once more; the macronucleus beginning to fragment. *F*, further fragmentation of the macronucleus, the wandering micronucleus passing from each Paramœcium into the other. *G*, union of the stationary and wandering micronuclei. *H*, a single Paramœcium after conjugation, the macronucleus degenerated, and the micronucleus beginning to divide. (Schematic representation based on the work of Maupas and Hertwig.)

active. Such, it may be recalled, is the condition in the sexual stage of the malarial parasite, Plasmodium, in which the sexual gametes resemble the ova and spermatozoa of the higher animals.

A departure from the usual mode of conjugation occurs in

Paramœcium, and most other Infusoria. In Paramœcium, in which the process has been most thoroughly studied, the individuals which pair become united for a time by their ventral, or oral, surfaces. While they are swimming about in pairs, several changes take place in their nuclei. The large meganucleus in each breaks up and degenerates. The micronucleus divides twice, forming four micronuclei, of which three degenerate; the remaining one divides once more into two nuclei, one of which passes over from each Paramœcium into the body of the other. The two Paramœcia thus exchange nuclei. In each individual the nucleus which is received from the other fuses with the nucleus which remains. It is perhaps not necessary for our purpose to describe the nuclear changes that take place in the Paramœcia after separation, further than to state that the single nucleus resulting from conjugation gives rise to both the micronucleus and the meganucleus of the individuals that are derived from each member of the conjugating pair.

In this complicated nuclear behavior there are certain features which recall the sexual reproduction of the higher animals. The divisions of the micronuclei preparatory to conjugation suggest the reducing divisions in the formation of the sex cells; and the union of the two micronuclei is, of course, comparable with what takes place in fertilization. Whether the division of the micronuclei actually effects a reduction in the number of chromosomes in Paramœcium is very difficult to ascertain. Unfortunately, little precise information has been gained concerning chromosome reduction in the one-celled organisms, although there are several facts which indicate that such a phenomenon occurs among them, much as it does in higher animals and plants.

Since the phenomena of sex are fundamentally similar in all sexually reproduced forms, it is probable that sex has much the same biological import for the life of the species, wherever it occurs. The problem of the significance of conjugation is but a part of the larger problem of the biological meaning of sex in general. Why should there be two sexes, anyway? Why could not organisms have perpetuated their kind with just females?

The very simplest organisms seem to get along very well, so far as we know, without sexual propagation. And there are species of higher organisms also that appear to reproduce exclusively without the aid of the male. It is easily possible to imagine a sexless organic world, but for some reason Nature has not seen fit to produce one. On the contrary, she has gone to a deal of trouble, to speak figuratively, in order to elaborate complex structures and modes of behavior in the service of sexual reproduction. One naturally suspects that there are very sound biological reasons for Nature's prodigality in this particular enterprise. What are the reasons?

One theory of the significance of sex that has often been applied in the interpretation of conjugation, is the so-called rejuvenescence theory. Continued asexual reproduction, according to this doctrine, leads to gradual deterioration. The French investigator, Maupas, brought forward what appeared to be strong support for this doctrine from his observations on conjugation in Infusoria. Cultures of these animals were found to propagate by fission for a long series of generations, sometimes as many as two or three hundred, but, at intervals, conjugation would take place, after which the course of reproduction would go on as before. Maupas observed that if individuals were kept from conjugating by isolating them as fast as they divided, the stock would gradually lose its vitality and ultimately die out. If, however, the infusorians were allowed to conjugate, the vitality of the strain was apparently restored, and its multiplication would proceed at an undiminished rate. Conjugation was considered to be a means of rejuvenating the run-down or senescent infusorians, which were supposed to have their periods of old age very much like higher organisms. These one-celled forms may be potentially immortal, but according to the rejuvenescence theory, they are potentially immortal in the sense that the ova and sperm cells are, whose continued life depends upon uniting with each other in fertilization.

A radically different theory of the significance of sexual reproduction has been elaborated by Professor Weismann. Sex, ac-

cording to this view, is not a means of rejuvenating cells that are otherwise destined to undergo natural death; it is a means of introducing variability into a species, and hence of endowing it with a plasticity and adaptiveness which enable it to meet the requirements of a changing environment. Sex would thus be an advantage to the species as a whole, instead of to the

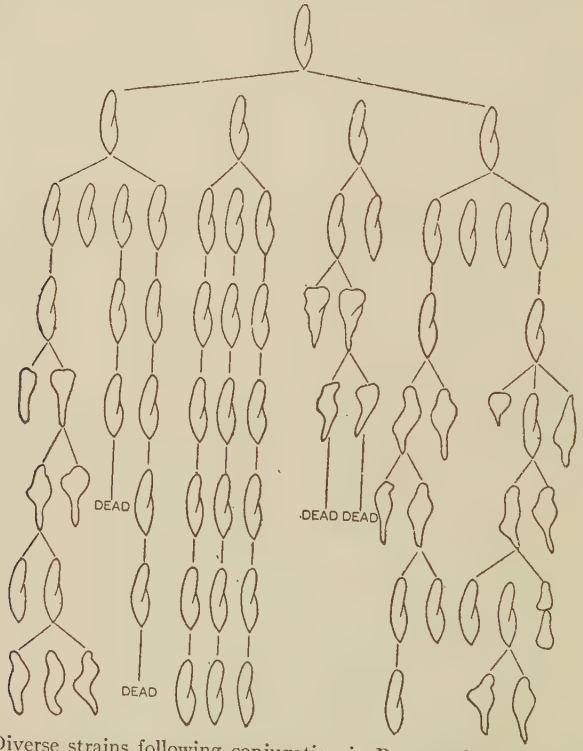

FIG. 94—Diverse strains following conjugation in Paramœcium. In the progeny of an ex-conjugant there are several abnormal strains. (After Stocking.)

individual organism. Its significance is evolutionary, rather than physiological.

There can be no doubt that the mingling of the germ plasms of different individuals produces a considerable degree of hereditary diversity among the offspring. Many illustrations of this fact will be adduced when we come to deal with the phenomena

of heredity. The same results, as Jennings has shown, follow conjugation in Paramœcium. The strains derived from individuals that have conjugated are more diversified than the ancestors of these conjugating individuals. Conjugation, in other words, appears to have induced variability. But does it also produce a rejuvenation of senescent individuals? Is there an element of truth in both views of the biological meaning of conjugation? The more recent work on conjugation is of particular interest in regard to these questions. Woodruff, with remarkable patience and assiduity, has kept a strain of Paramœcium without allowing the individuals to conjugate for over thirteen years, during which time it has produced over 8,500 successive generations! In keeping Paramœcia in a thriving state, it is found to be important to give them rather frequent changes of culture medium. Some of the signs of senescence formerly attributed to continued fission were probably the result of changes in the water in which the organisms were raised. The experiments of Woodruff, and other recent workers, indicate that, if properly handled, protozoans may reproduce by simple fission for a very long period of time. There are still differences of opinion concerning senescence and rejuvenescence. Woodruff has remarked, "There is no doubt that conjugation in certain cases directly results in stimulating all the vital processes of the cell, including reproduction," but he believes that the stimulating influence does not result so much from the fusion of nuclei as from the general nuclear reorganization that goes along with it. This change may be brought about without conjugation by a process which he called endomixis. In endomixis, which occurs periodically, the old meganucleus breaks up and a new one is formed by the division of the micronucleus which accompanies this process. Hartmann, however, has kept Eudorina for 600 generations without conjugation or anything resembling endomixis. This does not absolutely prove that this organism can keep on multiplying indefinitely in this way, but it strongly suggests it. In higher animals reproduction by budding or fission may be kept up for many years, and several plants

have been propagated asexually for centuries. That there is any natural limit to the process has never been proven.

The common reproductive cycle in unicellular organisms (except the very lowest) consists of a series of generations produced by fission, or some other asexual process, interrupted at intervals by conjugation. The same alternating cycle of sexual and asexual propagation is found throughout the higher plants and in a large part of the lower multicellular animals. The evolution of sex has been carried on in both plant and animal kingdoms, along diverging lines, but nevertheless these diverging developments show many interesting parallelisms. One instructive series of forms is presented by the colonial flagellate organisms, Pandorina, Eudorina, and Volvox. All of these forms consist of spherical colonies of chlorophyll-bearing cells, each of which is furnished at its outer end with a pair of flagella whose movements propel the colony, by a sort of rolling motion, through the water. In the simplest form, Pandorina, the colony consists of 16 to 32 cells imbedded in a jellylike mass. Ordinarily, asexual reproduction is brought about by each cell dividing into 2, 4, 8, 16, or 32 cells, thus forming small daughter colonies which escape from the jelly and then grow and reproduce

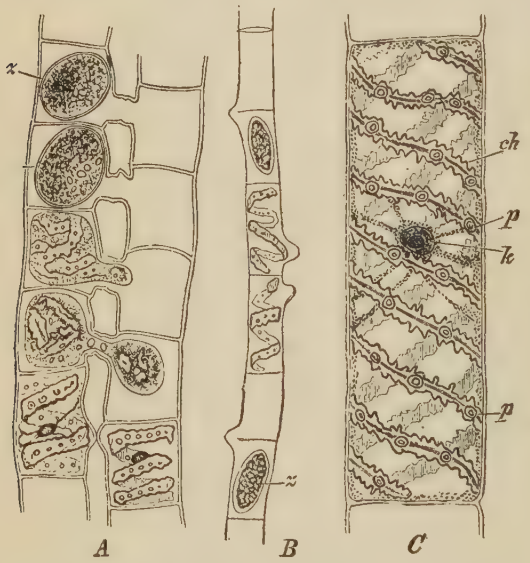

FIG. 95—Three species of a filamentous alga, Spirogyra: *A*, two parallel threads whose adjacent cells have become united, the protoplasm of the one having passed into the other and fused with the protoplasm of the invaded cell; *B*, *Spirogyra elongata; C*, *Spirogyra juvalis; ch*, spiral chromatophore; *k*, nucleus; *p*, pyrenoids; *z*, zygospore.

again in the same way. Propagation may go on by this means for many generations, but sooner or later there is a period of sexual union. The cells of the colony divide to form 16 or 32 cells, as before, but the individual cells are now liberated and swim about independently. They meet and fuse in pairs to form a zygote, which assumes a spherical form and develops a cyst within which it undergoes a resting period. After this it

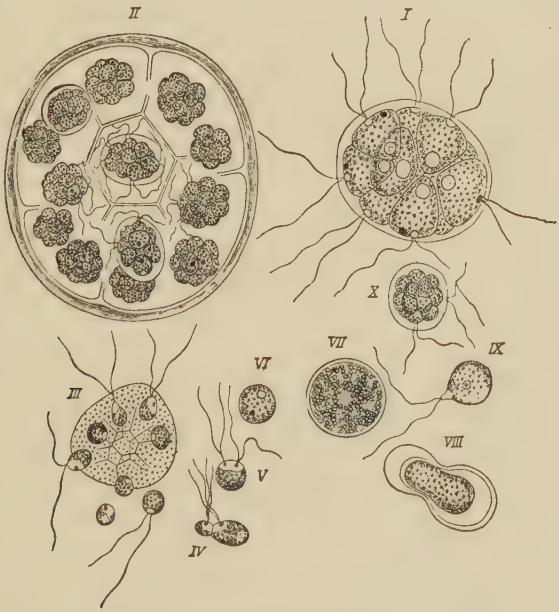

FIG. 96—*Pandorina morum: I*, free-swimming colony; *II*, division of each cell to form daughter colonies; *III*, a colony liberating free-swimming gametes; *IV*, *V*, conjugation of free gametes to form a zygote; *VI*, *VII*, *VIII*, *IX*, *X*, growth of the zygote and its development into a new colony. (After Pringsheim.)

divides to form a new colony, which continues to propagate for a further series of generations by the asexual method.

Eudorina is a colonial flagellate of sixteen to thirty-two cells, closely resembling Pandorina. Its asexual propagation is carried out in essentially the same way. At the sexual stage, however, two kinds of colonies make their appearance. One of these, the female colony, is composed of cells which are very much like

those of the ordinary type. The male colonies are distinguished by the fact that at maturity each cell divides repeatedly to form a plate of small flagellated cells, or microgametes. The plate is finally liberated and swims about until it comes into contact with a colony of the other sex, when the plate breaks apart into its component gametes, some of which fuse with the cells (macrogametes) of the female colony. Eudorina exhibits a well marked distinction between the male and female gametes, whereas in Pandorina the gametes are equal, or nearly equal in size. In both of these colonial organisms, however, all of the cells take part in reproduction; they are at the same time body cells and germ cells.

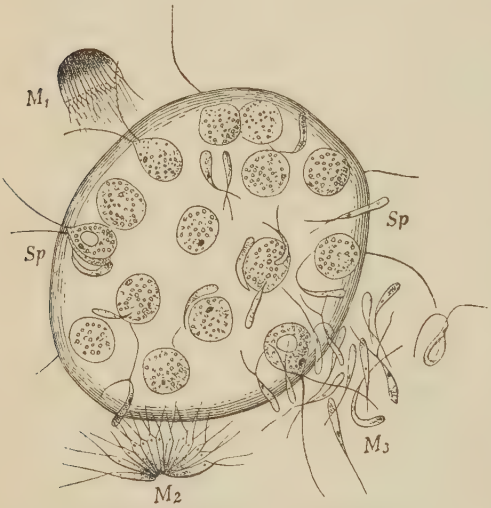

FIG. 97—*Eudorina elegans*, a free-swimming colony surrounded with gametes, M_1, M_2, M_3 *Sp*, from a male colony. (After Goebel.)

The third member of this series, Volvox, is a relatively large colonial organism, of about the diameter of a pinhead. The most common species, *V. globator*, often consists of many thousand cells. In this beautiful organism the cells are connected together by protoplasmic bridges, but they are all very uniform in size and form, with the exception of certain cells which are specialized for reproduction. In the usual method of reproduction, some of the cells enlarge, lose their flagella, and come to lie in the interior of the spherical colony. Here they divide to form daughter colonies, which are liberated by the rupture of the wall of the parental organism. These cells are said to develop by parthenogenesis, since they divide without being fertilized.

At intervals Volvox, like Pandorina and Eudorina, reproduces

sexually. Large, rounded female gametes are produced by the enlargement of some of the cells in the wall of the colony. Other cells of the same colony divide repeatedly to form small, mobile male gametes, much as in Eudorina. These break loose and fertilize the female sex cells, or ova. The zygote then forms a cyst, and, after a resting stage, develops into a new colony.

Volvox presents an advance beyond the two preceding forms, since, in addition to developing sex cells of different kinds, male and female, it exhibits a clear differentiation between the sex cells, which are potentially immortal, and the somatic, or body cells, which are destined sooner or later to perish. Coincident with this differentiation between sex cells and soma, we have the advent of natural death, a fate which does not overtake the cells of Pandorina or Eudorina, all of which, at least theoretically, may go on dividing forever.

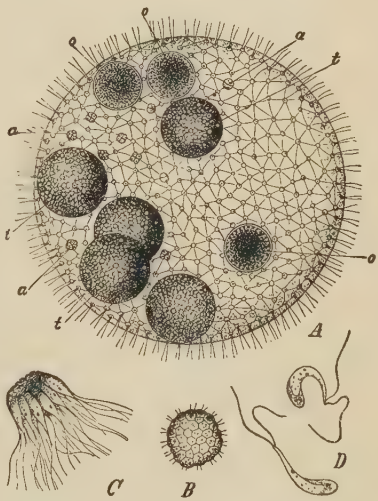

FIG. 98—*Volvox globator: A*, mature colony; *a*, developing spermatozoa; *o*, ova; *l*, daughter colonies on the inside of the organism. *B*, *C*, two stages in the development of spermatozoa; *D*, mature spermatozoa. (After Klein and Schenck.)

Among the simpler multicellular plants, such as the algæ and fungi, we meet with various stages in the evolution of sex. One of the common molds, *Mucor mucedo*, which often appears on bread and vegetables, affords an illustration of a plant with relatively simple asexual and sexual modes of reproduction. If we examine the whitish patches of this mold with a microscope, we may observe a mass of branching threads (mycelium) from which arises a beautiful forest of upright stalks, each bearing a spherical enlargement at its tip. This enlargement is a spore case in which are developed numerous rounded and thick-walled spores which are liberated by the rupture of the wall of the case.

The germination of these spores affords the ordinary means of asexual propagation. The sexual process is first manifested by two short stalks growing toward each other from near-by threads. When the tips of the threads meet, a cell is cut off near the end of each by a transverse septum, the adjacent cell walls disappear and allow the contents of the two cells to intermingle. A new wall forms around the combined protoplasmic masses and incloses the zygote, which subsequently germinates into a new

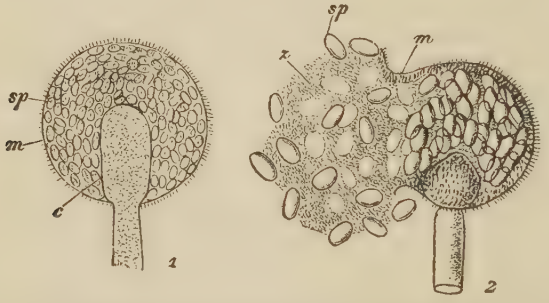

FIG. 99—Development and discharge of spores in the sporocyst of the mold *Mucor mucedo: c*, stalk; *m*, wall; *sp*, spores; *z*, mucilaginous substance between the spores.

threadlike plant (Fig. 100). In many other molds the conjugating cells are of unequal size.

As an example of a somewhat more complex reproductive cycle, we may select the common fern, *Aspidium felix-mas*. The life cycle of the fern is divided into two alternate generations, represented by plants of very different appearance. The commonly observed form of the fern plant, with its graceful pinnate leaves, or fronds, arising from a subterranean root-stalk, represents the sporophyte, or spore-bearing generation. On the lower surface of some of the mature fronds one may observe the brownish clusters of stalked spore cases, or sporangia. Within these sporangia are developed the rounded spores, which are liberated by the rupture of the inclosing wall. Under suitable conditions the spores germinate, giving rise to a small, green plate of cells about a quarter of an inch in diameter, called the prothallus. The fine rootlets which grow out from the lower surface of the prothallus serve to imbibe nutriment from the

soil, and the chlorophyll of the exposed surface enables the plant to elaborate the absorbed material by the usual method of photosynthesis. The prothallus constitutes the sexual, or gametophyte generation, which is so called because it produces the sex cells, or gametes, which are formed in special organs situated on its lower surface. The female sex cells are formed in organs called archegonia, each of which consists essentially of a short column of cells with a central tubular cavity at the bottom of which is the female gamete, or egg cell. The antheridia, or organs giving rise to the male cells, are somewhat similar in form to the archegonia, but they give rise to a large number of small, motile male gametes, which, after they are liberated, swim about in the moisture on the lower side of the prothallus. They are drawn into the archegonia by a secretion produced in these organs and effect the fertilization of the egg cells.

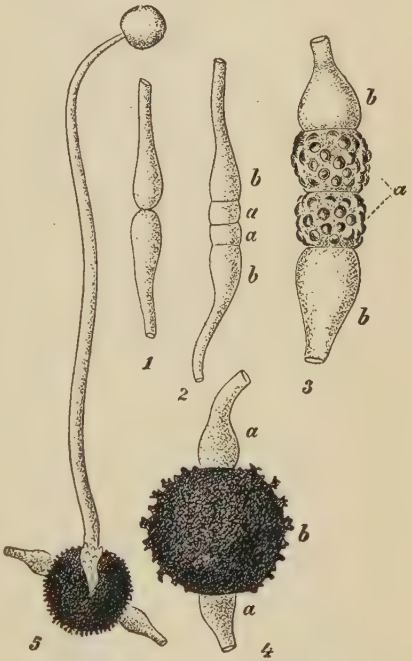

FIG. 100 — Sexual reproduction in the mold *Mucor mucedo: 1*, two conjugating branches meeting at their tips; *2*, formation of a cell, *a*, *a*, at the end of each branch *b*, *b; 3*, more advanced stages of the conjugating cells; *4*, the two conjugating cells have fused together to form a zygospore, *b; 5*, germination of the zygospore, the thread bearing a spore case at its tip. (After Brefeld.)

The fertilized ovum is not discharged from the archegonium, but germinates in its original position. The plant thus formed is the young sporophyte. At first it draws its sustenance from the prothallus, but later, developing roots and fronds of its own, soon outgrows the small prothallus, which withers up and disappears. There are several species of ferns in which the male

and female sex cells are produced in separate prothalli. Often the prothalli of the two sexes are developed from different kinds of asexual spores, the female prothalli coming from relatively large spores, the megaspores, while the male prothalli develop from the smaller microspores. This difference in the spores and the gametophytes to which they give rise, is of especial interest on account of its relation to the life cycle of the flowering plants.

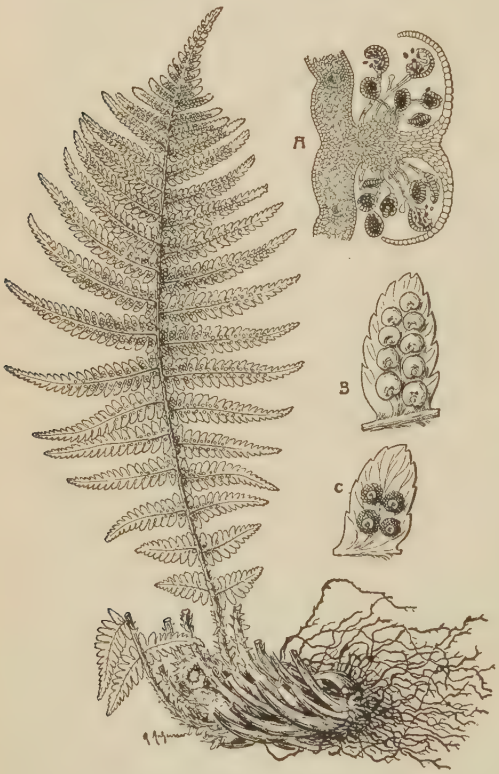

FIG. 101—The fern *Aspidium felix-mas: A*, cross-section of a part of a leaf showing stalk spore cases, some of which are discharging spores; *B, C*, the under surfaces of leaflets with sori containing spore cases. (From Strasburger.)

Ordinarily one would not suspect the flowering plants of passing through two very different generations in the course of their life history. The seeds of corn or beans, which we gather directly from their respective plants, give rise again to corn and bean plants. Careful microscopical study of the stages of generation in the flowering plants has revealed, however, that there is a true alternation of sporophyte and gametophyte generations, as there is in the mosses and ferns, but that the gametophyte is so effectively concealed within the sporophyte that it requires very close scrutiny to discover it. In other words, the two generations have become telescoped

together, and one of them has been very greatly reduced in size.

In order to follow the reproductive cycle of the flowering plants, it is necessary to consider briefly the structure of the flower, a topic which we omitted while describing the green plants. A typical flower consists of four sets, or whorls, of organs. The lower and outer set, called the calyx, is composed of several, usually green, sepals. Within these are the petals which constitute the corolla. The next set of organs is composed of the stamens, each of which consists of a slender filament, or stalk, bearing at its summit the anther which contains

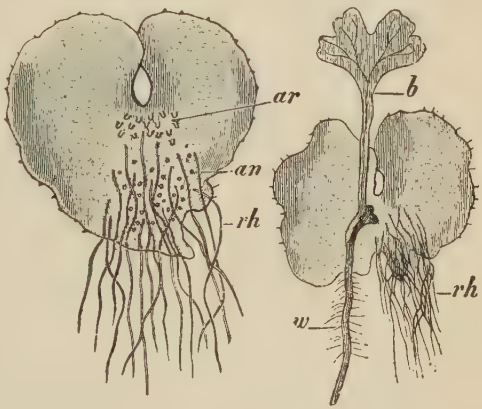

FIG. 102—Prothalli of the fern *Aspidium felix-mas* seen from the lower surface: *an*, antheridia; *ar*, archegonia; *b*, young fern plant still attached to the prothallus; *rh*, rootlets; *w*, root of young fern. (From Strasburger.)

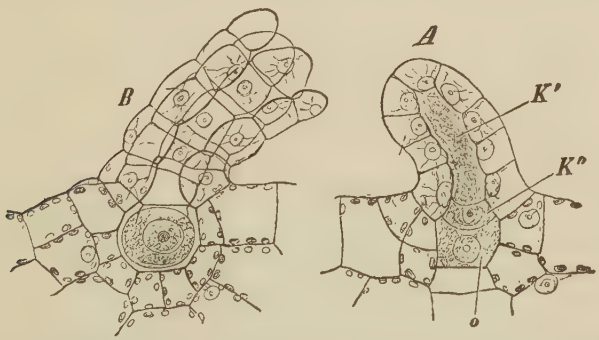

FIG. 103—Archegonia of the fern *Polypodium vulgare: A*, young archegonium not yet open; *K'*, *K''*, canal cells; *o*, ovum; *B*, mature open archegonium. (After Strasburger.)

the pollen grains. The terminal and most internal set of organs is composed of the pistils, which are sometimes separate and some-

times united into a single organ. A pistil includes (1) an enlarged basal part, the ovary, (2) a style which extends above it, and (3) a terminal stigma which is frequently adhesive and thus adapted to retain the pollen grains which may be deposited upon its surface. The ovary contains several bodies called ovules, which give rise to the seed. Within each ovule is a large megaspore, which is also known as the embryo sac. The megaspore is not liberated, but it develops *in situ* into a female gametophyte. This generation is so extremely reduced that it consists of a very few cells within the wall of the megaspore. Only one of these cells represents the true female gamete, the others representing the very rudimentary soma of the sexual, or gametophyte, generation. It is this cell which is fertilized by a corresponding male gamete derived from the pollen grain. The pollen grains were formerly considered to be male gametes, corresponding to the spermatozoa of animals, but they are really microspores. The mode in which fertilization is effected in flowering plants is as follows:

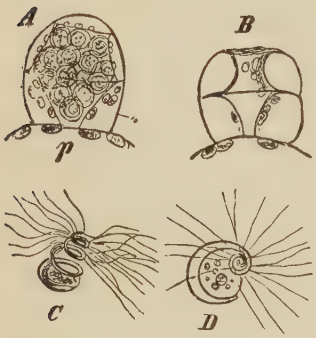

FIG. 104—Antheridia of *Polypodium vulgare: A*, mature, *B*, empty antheridium; *C*, *D*, spermatozoids. (After Strasburger.)

FIG. 105—Two flowers cut in two lengthwise, the upper with a single style, the lower one with several. (After Gray.)

When the pollen grains are deposited upon the moist surface of the stigma, they germinate by pushing out a tubular process, which grows down through the tissues of the style until it comes into contact with one of the ovules. During the growth

of the pollen tube, the single nucleus of the pollen grain divides into two, one nucleus passing into the tube, the other remaining behind. The nucleus of the tube again divides. As the pollen tube penetrates the ovule it passes into the embryo sac and one of its two nuclei unites with the nucleus of the female gamete. The other nucleus unites with one of the other nuclei of the female gametophyte known as the endosperm nucleus. There is thus accomplished a sort of double fertilization. From the one union arise the tissues of the embryo plant, and from the other the part of the seed known as the endosperm. The pollen grain, as we have said, is a spore, and the few divisions which its nucleus undergoes represent its germination to form the male gametophyte. Of the three nuclei of this body, only one might be said to represent the soma of this generation. The other two correspond to its germ cells. The male gametophyte, which is reduced almost to the vanishing point, represents the last remnant of a long process of degenerative development. Among the liverworts and mosses, the gametophyte is larger than the sporophyte, and the latter leads a sort of

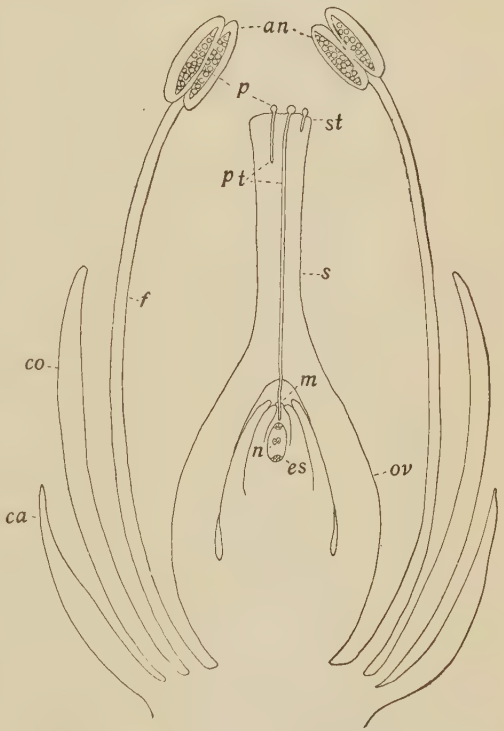

FIG. 106—Diagram of a longitudinal section through a flower illustrating the process of fertilization: *an*, anthers; *ca*, calyx; *co*, corolla; *es*, embryo sac; *f*, filament of stamen; *m*, micropyle; *n*, nuclei of embryo sac; *ov*, ovary; *p*, pollen grains in the anther and on the stigma; *pt*, pollen tubes; *s*, style; *st*, stigma.

dependent existence upon the former. During the long evolution of the higher plants, the tables have been turned, and it is the gametophyte that is all but completely swallowed up within the sporophyte.

The stamens and pistils are sometimes designated as the essential organs of the flower, because they bear the pollen grains and ovules, which are used in the production of seed. In appearance they are very different from the other parts by which they are surrounded. Nevertheless there is a common plan of structure among all these floral organs which has led botanists to regard them as homologous parts. The poet Goethe, in his essay on "The Metamorphoses of Plants," put forward the view that the sepals, petals, stamens, and pistils of a flower are all modified leaves which have been transformed to a greater or less extent in adaptation to their different functions. Goethe supported this fascinating generalization by an array of convincing facts, and botanists have since come to regard it quite generally with favor. The resemblance between leaves and the green sepals of a flower is sufficiently obvious. Often sepals and petals are very similar to each other in form and color, and there can be little doubt that they represent homologous parts. The stamens are more highly specialized organs, but if you examine the petals of a pond lily or a double rose, you may find every transitional stage between stamens and petals. The carpels, or compartments of the pistil, may be considered as composed each of an enfolded leaf, or sporophyll, whose approximated edges bear the megaspores. Stamens and pistils thus have their representatives in the spore-bearing leaves, or fronds of the so-called flowerless plants.

FIG. 107—The transition between sepals, petals, and stamens seen in the flower of the white pond lily. (After Gray.)

The petals and sepals of a flower are in part protective envel-

opes for the stamens and pistils, but they serve also, especially the petals, as accessories to the process of reproduction. The usual interpretation of the meaning of the bright color of flowers is that it serves as a means of attracting insects. Flowers and insects present a great variety of mutual adaptations by which insects are enabled to obtain nectar from the flowers and the flowers in turn are cross-fertilized by their insect visitors. Near the close of the eighteenth century, the thoughtful German naturalist Sprengel published a work in which he explained many of the structural features of flowers as special contrivances for the convenience of visiting insects. Sprengel's researches, however, did not attract a great deal of attention on the part of his contemporaries. The significance of the interrelationship of flowers and insects was not adequately appreciated until the subject was illuminated by the painstaking and ingenious investigations of Charles Darwin. Flowers and insects, according to Darwin, have been evolved together, and each has influenced more or less profoundly the evolution of the other. The nectar which is commonly secreted near the base of flowers is eagerly sought after by numerous insects, and the odor and bright color of the flower serve to apprise the insects of the whereabouts of their coveted food. While the flower offers its sweets to the insects, it is commonly so fashioned that some of its pollen gets dusted upon the body of its insect visitors, and when the insect carries the pollen to another flower it brushes off some of the grains upon the stigma of the pistil.

An excellent illustration of how this transfer of pollen is effected is furnished by the blossom of the common sage, *Salvia pratensis*. The irregular bilobed corolla is furnished with a sort of platform upon which insects may readily alight preparatory to entering the tubular part of the corolla which contains the nectar at its base. The stamens of the sage blossom are attached so that they may be moved by a sort of hinged joint near their point of attachment. The insect passing into the tube of the flower presses against a short projection at the base of the stamens, and thereby causes the anthers to be bent down

so as to dust pollen on the insect's back. The pistil, like the stamens, lies beneath the upper part of the corolla. When it is mature it projects in such a way that it is apt to receive some of the pollen carried on the back of a visiting insect from another flower. In this manner the flowers are commonly cross-fertilized by pollen from a different plant, or at least from a different blossom, and the process of self-fertilization is prevented by the circumstance that the stamens mature and discharge their pollen before the pistil is ready to receive it.

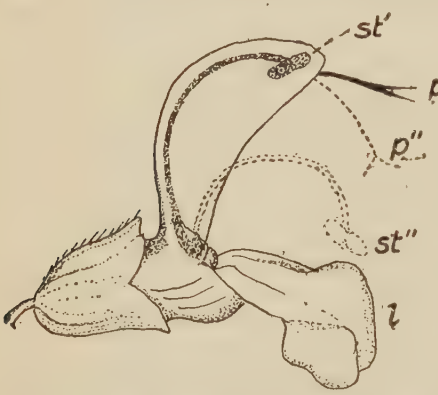

FIG. 108—Sage blossom: *l*, lower lip of the corolla; *p'*, pistil in immature state; p'', the position of the pistil when mature; *st'*, stamen in normal position; *st''*, position assumed by the stamen as a result of the entrance of an insect into the tube of the corolla.

Most remarkable devices for securing cross-fertilization through the agency of insects, have been described by Darwin in his works on *The Effects of Cross and Self Fertilization in the Vegetable Kingdom*, and on *The Fertilization of Orchids*. There are many plants, as Darwin showed, which fail to set seed unless they are fertilized by pollen from another plant. This is commonly the case in ordinary red clover. Many kinds of plants bear either pistillate flowers only, or staminate flowers only, so they must of necessity be fertilized by foreign pollen.

Most of the plants which are cross-fertilized by pollen carried by the wind, such as oaks, willows, alders, grasses, and sedges, have relatively small, inconspicuous, and odorless flowers, often devoid of petals, and commonly lacking in nectar. Nature has spent little effort upon their adornment, but she has usually furnished them with a profusion of pollen. Insect pollination is in some respects more economical, but it costs more in advertisement and bait. If all the devices to secure cross-ferti-

lization have not been in vain, it must have some important significance in the life of the species. What is it? This question greatly interested Mr. Darwin, and he performed numerous experiments in order to find out the answer. Many of his investigations were designed to test the relative vigor and fertility of the progeny of self-fertilized and cross-fertilized plants. One of his typical experiments he describes as follows:

Six crossed and six self-fertilised seeds of *Ipomœa purpurea*, from plants treated in the manner above described, were planted as soon as they had germinated, in pairs on opposite sides of two pots, and rods of equal thickness were given them to twine up. Five of the crossed plants grew from the first more quickly than the opposed self-fertilised plants; the sixth, however, was weakly and was for a time beaten, but at last its sounder constitution prevailed and it shot ahead of its antagonist. As soon as each crossed plant reached the top of its seven-foot rod its fellow was measured and the result was that, when the crossed plants were seven feet high the self-fertilised had attained the average height of only five feet four and a half inches. The crossed plants flowered a little before, and more profusely than the self-fertilised plants. On opposite sides of another small pot a large number of crossed and self-fertilised seeds were sown, so that they had to struggle for bare existence; a single rod was given to each lot: here again the crossed plants showed from the first their advantage; they never quite reached the summit of the seven-foot rod, but relatively to the self-fertilised plants their average height was as seven feet to five feet two inches. The experiment was repeated during several succeeding generations, treated in exactly the same manner, and with nearly the same result. In the second generation, the crossed plants, which were again crossed, produced 121 seed-capsules, whilst the self-fertilised, again self-fertilised, produced only 84 capsules.

This result is typical of numerous others which Darwin describes. Many flowers were found to be infertile when impregnated by their own pollen. On the other hand, several species, including our common varieties of beans and peas, are quite regularly self-fertilized; but Darwin maintains that cross-fertilization in nearly all cases occasionally occurs. "Nature,"

he says, "abhors perpetual self-fertilisation." The mingling of slightly different germ plasms was supposed to produce enhanced growth and vigor, while self-fertilization and close inbreeding bring about in time a deterioration of the stock. The devices of plants to secure cross-fertilization were therefore considered as highly beneficial endowments. In one way or another they doubtless are.

The phenomena of sex in animals are essentially similar to those of plants. In all the multicellular animals there is a marked distinction between male and female gametes. The fresh-water Hydra, for instance, which is one of the simpler metazoans, produces relatively large egg cells beneath the ectoderm near the basal part of the body. The growing ovum becomes a large amœboid cell, which engulfs and assimilates the smaller cells around it. Finally, when it is ready to be fertilized, it protrudes as a rounded body from its ectodermic covering. The small active sperm cells of Hydra are produced in conical prominences near the tentacles, and when mature they break out and one of them succeeds in fertilizing the egg, which then develops for a time while still connected with the body. The outer layer of the developing egg secretes a chitinous covering, or capsule, within which the egg may remain in a dormant state for some time after it drops off from the body. Often Hydras winter over in this capsule and complete their development at a later and more favorable period. The bursting of the capsule frees the young Hydra, which rapidly grows and assumes its normal form.

Many of the relatives of Hydra, the hydroids, give rise by budding to a very different generation, known as a medusa, or jellyfish. In typical cases the jellyfish is set free and swims about in the water. It represents the sexual generation and produces ova, or sperms, usually in different individuals. The fertilized eggs develop not into medusæ, but into hydroids, so that there is an alternation of sexual and asexual generations. In many hydroids the medusæ are never set free, and in some instances they become very much reduced or degenerate in structure. Their

fate is, therefore, quite analogous to that of the gametophyte, or sexual generation, in the higher plants.

Most of the simpler multicellular animals shed their sex cells into the water and leave their union to chance. Among most of the fishes, the male has the instinct to keep close by the female during the breeding season, and when the eggs are deposited he

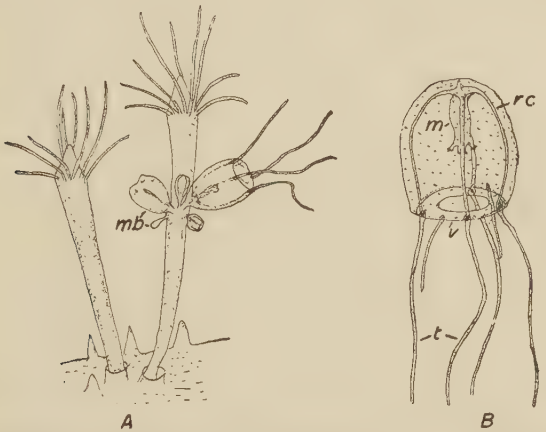

FIG. 109—Alternation of generations in Hydromedusæ: *A*, a hydroid; *mb*, medusa bud; *B*, the free jellyfish stage; *m*, manubrium; *rc*, radial canals; *t*, tentacles. (After Allmann.)

discharges his milt, or sperm, over them. The male frogs and toads clasp the female during the breeding season and shed their sperm over the eggs as soon as they are laid. From such procedures for securing fertilization, it is not a long step to fertilization within the body of the female. This occurs in all higher vertebrates, *i. e.*, the reptiles, birds, and mammals, as well as in some of the fishes and amphibians. It is the common method of fertilization in the higher invertebrate animals, such as the crustaceans, insects, spiders, and many groups among the worms and

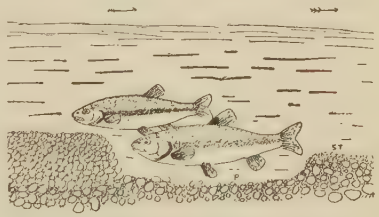

FIG. 110—Male and female of the horned dace in nest where the eggs are laid and fertilized. (After Reighard.)

molluscs. The development of fertilization within the body makes possible an economy of the sex cells, because there is much less waste involved, and the fertilized eggs may be protected for a longer or shorter time within the maternal organism. In nearly all mammals, as everyone knows, development takes place within the uterus of the mother. There is one small order of mammals, however, the monotremes, consisting of the Australian duckbill and the spiny anteater, both of which lay eggs. In the marsupials, which stand next above the monotremes in the developmental scale, the young are born in a very immature state and are carried about for a time in a brood pouch on the ventral side of their mother's body. Here they derive milk from the mammary glands and develop until they become quite lively young animals.

Development within the body of the higher mammals involves the formation of a special organ called the placenta, by which the young embryo is attached to the walls of the uterus. Through the placenta the embryo derives the material for its growth. The blood vessels belonging to the circulatory system that is formed in the embryo are intimately associated in the placenta with the maternal blood vessels, but all materials passing from one set of vessels to the other must pass by osmosis through the intervening membranous walls. The maternal blood furnishes oxygen and food to the embryo and receives in turn the waste products of the metabolism of the embryo. The mother must not only partake of food for herself and her offspring, but also eliminate the waste products of both.

Internal fertilization has had many important consequences for the further evolution of animal life, because it has made possible the development of the higher forms of peculiarly terrestrial animals. The egg cells require a fluid medium for successful fertilization. Hence they must be fertilized either within the water or within the animal where they are kept moist by the fluids of the body. Frogs, toads, and other amphibians are usually not completely terrestrial, owing to the fact that their eggs are fertilized outside the body; hence these animals are forced to

repair to the water during the breeding season. The Amphibia, as the name implies, are transitional types between aquatic and terrestrial animals. In all of the higher classes of vertebrates, the eggs are fertilized within the body, a circumstance which enables these animals to become completely emancipated from their dependence on an aquatic habitat. A few groups among the higher vertebrates (whales, seals, penguins, turtles, sea snakes, etc.) have come to be dependent, to a greater or less degree, upon an aquatic mode of life, but they represent forms which have gone back to the water again after they had become adapted to life upon land.

The necessity for fertilizing the eggs before or immediately after their discharge from the body has entailed the development of mating instincts which bring about the contact of the two sexes. In mating, the male has assumed the more active rôle. In the service of this function males are not only furnished with copulatory organs, but frequently also with various organs for enabling them to find the opposite sex. Hence their frequent endowment with superior organs of sense. The males of many kinds of moths possess large feathered antennæ which are much more elaborately developed than those of the female. In the insects the antennæ are the chief organs of the sense of smell, and it is by means of this sense that the male moths are attracted to the females, which they are able to recognize at a great distance. In one of Fabre's most entertaining essays on the habits of insects, there is an account of the mating behavior of the large moth, which, on account of the ornamentation of its wings, has received the name "the Great Peacock." A cocoon kept in the study of the celebrated naturalist had given rise to a female moth, which was kept under a cover of gauze. In the evening the house was invaded by a multitude of male moths. "Come from all points of the compass, warned I know not how, here were forty lovers eager to do homage to the maiden princess born within the sacred precincts of my study." Although the night was one of black darkness the male moths found their way through the surrounding trees and into the open windows, drawn by their

keen olfactory sense for the substances diffusing from the recently emerged female. This occurrence led Fabre to make several experiments on the moth's sense of smell. "When," he says, "I placed the females in boxes which were imperfectly closed, or which had chinks in their sides, or even had them in a drawer or cupboard, I found the males arriving in numbers as great as when the object of their search lay in the cage of openwork freely exposed on a table. I have a vivid memory of one evening when the recluse was hidden in a hatbox at the bottom of a wall cupboard. The arrivals went straight to the closed doors and beat them with their wings, toc-toc, trying to enter. Wandering pilgrims come I know not where across fields and meadows, they knew perfectly what was behind the doors of the cupboard."

FIG. 111—Eyes of honey bees: *A*, queen; *B*, drone. (After Cheshire.)

In many instances the males are distinguished from the females by their superior organs of vision. The compound eyes of the drone bee are considerably larger than those of the queen or worker. There are sometimes similar sex differences in the organs of hearing, as in the mosquitoes, in which the males are furnished with a well developed apparatus for the detection of sound, particularly the hum of the female. Sounds, like smells, afford a much employed means of sexual attraction, and the males of many forms are equipped with various kinds of apparatus for producing noises by which they may advertise their presence,

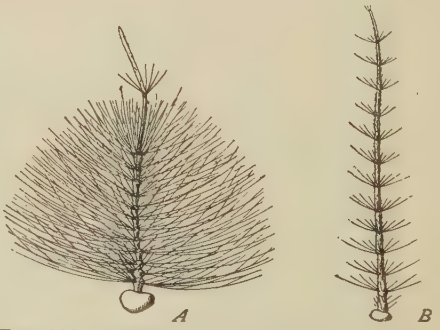

FIG. 112—Antennæ of the mosquito, *Culex pipiens: A*, male; *B*, female.

and perhaps exercise an alluring influence upon their prospective mates. The males of several species of grasshoppers produce their strident notes by rubbing their large hind legs across one or more of the specialized veins of the outer wings. Among the crickets and katydids, the males possess a stridulating organ near the base of the wings. By elevating the wings somewhat and rubbing the one over the other, the males produce the characteristic chirping sounds by which they carry on their

FIG. 113—Wings of the cricket, *Gryllus assimilis:* left figure, wing of female; right figure, wing of male showing modifications of veins for the production of musical notes.

industrious courtships. The male cicadas, or harvest flies, have a very different musical apparatus situated on either side of the base of the abdomen.

In the vertebrates the sound-producing organs are developed in connection with the organs of respiration, and the sounds are made by chords which are set into vibration by means of the air expelled from the lungs. The production of sound is hence limited chiefly to terrestrial, air-breathing forms. The croaking of frogs and the notes emitted by tree toads are chiefly the performances of the males, whose sounds greatly exceed in volume the weak vocal efforts which are more rarely made by the females. The vociferous calls of the male amphibians are mainly confined to the breeding season, and their function is that of bringing

the two sexes together. Their efficacy in this respect is evinced by the fact that the females have been found to seek the places from which the sounds of the males proceed.

The vocal apparatus is found in both sexes in birds, although it is usually better developed in the males, especially among the song birds. Its function, as in the Amphibia, is primarily a sex call, although it is employed also for warning cries, and calls to the young. It is during the period of courtship that the male song bird outdoes himself in his efforts at vocal display.

Among other sex differences evolved in the service of mating,

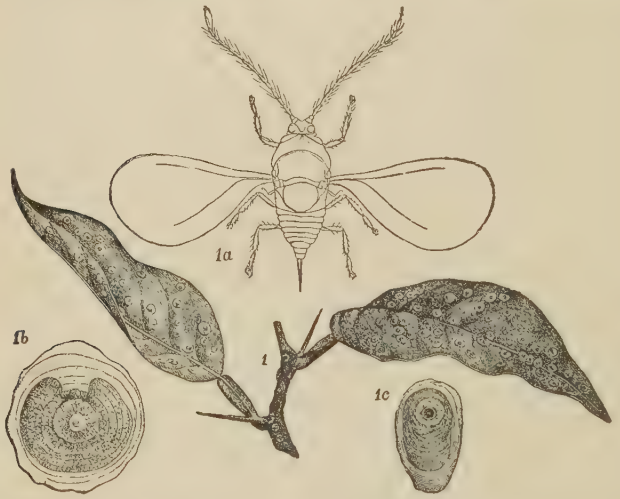

FIG. 114—The red scale *Aspidiotus aurantii: 1*, scales on orange leaves, three-fourths natural size; *1a*, the mature male; *1b*, the mature female scale insect magnified; *1c*, immature scale of male, magnified. (After Comstock.)

may be mentioned the greater activity and more complex organization that frequently characterizes the male sex. In the adult scale bugs, for instance, the female is a degenerate creature attached to the plant upon which she feeds. She is devoid of wings, legs, eyes, and various other organs not directly connected with the functions of alimentation and reproduction, which constitute her main business in life. The male, the chief end of whose existence is to find and fertilize the female, is an active,

graceful insect, furnished with legs, wings, and well developed sense organs. The females of some parasitic isopod crustaceans are so degenerate in structure that they appear to be little more than amorphous egg-producing sacs, but the males retain the highly organized form that is typical of the group to which they belong. The female glow worm, although a true beetle, is devoid of wings, while the male has well developed wings and wing cases.

In many animals the males are provided with special organs for seizing and holding the female. The male brine shrimp Artemia has his second antennæ enlarged and specially modified for this purpose. The forelegs of the male water beetle, *Dytiscus marginalis*, are furnished with several suckers on the inner surface of the expanded joints. Male frogs and toads have the inner digit of the forelegs enlarged and swollen at the base, and the musculature of the forearm is more fully developed than in the other sex, in obvious adaptation to the clasping function during the breeding season.

A part of the special equipment of the male sex has an evident relation to the battles that are waged for the possession of the females. The instinct to provide for the possible continuation of his kind is one of the strongest propensities of the male sex, and the rivalries that inevitably arise in regard to what males are privileged to perpetuate their qualities afford the occasion for frequent conflicts. The perpetuation of life is a part of "the will to live," and Nature has made the male a jealous guardian of his stream of life. She has equipped the cock with his sharp spurs, the male deer with his antlers, the male lion with his protective mane, and caused the males of many species to exceed the females in size, strength, and pugnacity. During the breeding season the males of many kinds of mammals are animated by a deadly hostility to all possible rivals. The bull moose, with his new equipment of well hardened antlers, which have been maturing during the spring and summer, goes forth in the fall to seek the females, that he previously regarded with indifference. Now he is maddened with an overmastering sexual de-

sire and at times he issues his challenging cry, frequently stopping to listen for the fainter response of the females. The males that hear each other's challenge make all haste to rush into conflict and death is often the lot of the vanquished. Among deer, antelopes, horses, cattle, elephants, and swine, a single male frequently dominates the herd and fights away all rivals until some stronger contestant successfully disputes his supremacy. At the breeding season the stronger male, or "bull," sea lions possess themselves of a harem of "cows" that they jealously guard. A cow that attempts to escape is followed and driven, or sometimes carried, back into the fold. If she seeks refuge in the harem of another bull, she becomes a bone of contention and may be torn to pieces by the rival males. A bull sea lion must be on the alert to maintain his position of dominance and to prevent the desertion of his cows to some of the smaller or weaker males that congregate at a safe distance around the outskirts of the herd.

In several groups of the higher animals, the males are distinguished by their more brilliant coloration and the possession of special ornamental structures. Animals possessing these ornaments often have instincts for displaying them in the most effective manner. The gorgeous plumage of the male peacock, lyre bird, and bird of paradise affords striking instances of such sexual dimorphism. In the period of courtship the male birds eagerly display their charms before their prospective mates. "The bull finch," says Darwin, "makes his advances in front of the female and then puffs out his breast so that many more of the crimson feathers are seen at once than otherwise would be the case. At the same time he twists and bows his black

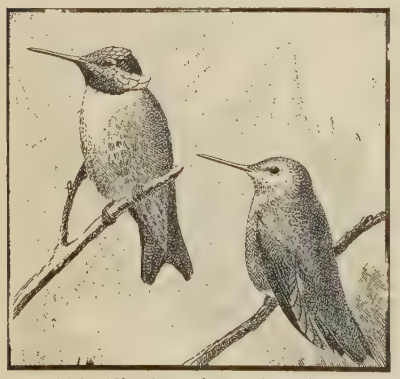

Fig. 115—The Anna humming-bird: male at left, female at right. (After Beal and McAtee.)

tail from side to side in a ludicrous manner. The male chaffinch also stands in front of the female, thus showing his red breast and blue bell as the fanciers call his head; the wings at the same time being slightly expanded with the pure white band on the shoulders thus rendered conspicuous. The common linnet distends his rosy breast, slightly expands his brown wings and tail, so as to make the most of them by exhibiting their white edgings."

For the explanation of the differences in ornamentation and

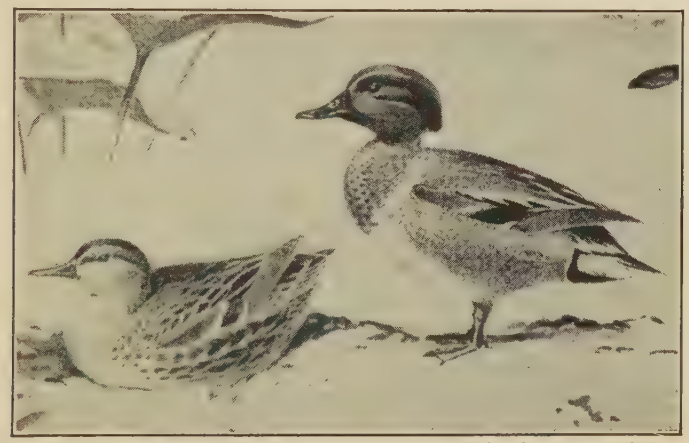

FIG. 116—Green-winged teal duck: male at right, female at left.

many other sexual characters we have described, Mr. Darwin has propounded his celebrated theory of sexual selection. According to this doctrine the males that are the more successful in battle, as a result of superior strength or better equipment of horns, teeth, or other weapons would be the ones that would be apt to leave the most progeny to inherit their superior endowments. As a result of the continued selection of the stronger or better armed contestants, the peculiar characteristics of the male sex were gradually evolved. For the explanation of the development of superior ornamentation or powers of song, Darwin supposes that the females are apt to choose the most attractive of their rival suitors, and thus, through cumulative selection in numerous generations, to produce the brilliant colors

and other attractive qualities of the more ornamental sex. Several instances have been adduced by Darwin and others in which females have chosen the more brilliant among the candidates for their favor. Darwin quotes Weir to the effect that "a female pigeon will occasionally take a strong fancy for a particular male, and will desert her own mate for him," and he cites a case of "a male silver pheasant, who had been triumphant over all other males, and was the accepted lover of the females, had his ornamental plumage spoiled. He was then immediately superseded by a rival who got the upper hand and afterwards led the flock."

Notwithstanding many cases of obvious selection on the part of female birds, there is much difference of opinion over Darwin's explanation of those sex differences which are supposed to be the outcome of female choice, although his theory of the origin of the fighting equipment of the males is generally adopted.

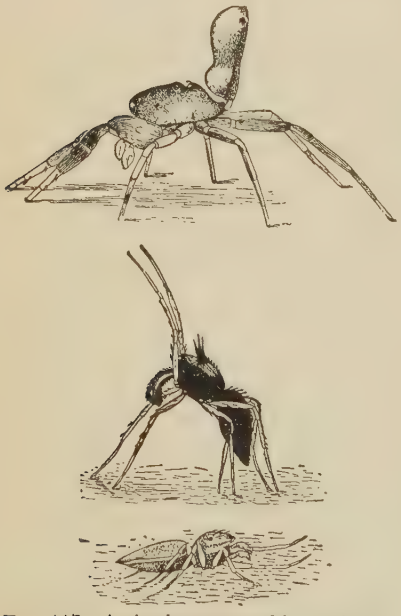

FIG. 117—Attitudes assumed by male spiders during courtship. (After Peckham.)

One would not expect to meet with the ceremonies of courtship among primitive forms of animal life. But when we come to such highly organized creatures as scorpions and spiders, we find that mating is preceded by a more or less elaborate wooing. The males of the jumping spiders commonly dance about the females in a most amusing manner, swaying the body from side to side, and often waving their palpi and forelegs about in the air. In the orb-weaving spiders, the males are generally many times smaller than the females, and they have to make

their amorous approaches with great caution. The females, being predatory and rapacious, are apt not to discriminate between the males and the other small creatures that constitute their accustomed prey. The males are therefore frequently devoured in their efforts to impregnate the females. Courtship among spiders consists apparently in a series of acts by which the male wins over the female to accept his advances. Perhaps the colors with which the males of several species of spiders are adorned may serve as signs of maleness instead of appealing to the æsthetic sense, which we can hardly suppose to be well developed in a creature of such limited mentality and savage character as a female spider. Perhaps, also, the appeal of male ornamentation in the birds and mammals may rest upon much the same basis.

Notwithstanding the efforts of Nature to insure that her organisms shall be the product of two parents instead of one, we find that many species are able to propagate without the services of the male sex. The development of eggs without fertilization is a process known as parthenogenesis, a word which means virgin reproduction. Parthenogenesis occurs occasionally in plants and in the invertebrate animals, but it is not found normally in the vertebrates. In most animals that propagate in this manner, there is one or more parthenogenetic generations, and then a sexual generation in which the eggs are fertilized in the usual way.

The small crustaceans known as water fleas (Daphnidæ) commonly reproduce for several generations from small, so-called summer eggs, which develop without fertilization. Several of these eggs are carried in the maternal brood pouch and they usually develop into females. There may be several generations in which only females are produced, but finally males also make their appearance. At this time the females may produce eggs of a different character, fewer, larger, and requiring to be fertilized before they develop. These are the so-called winter eggs, and they may withstand cold or drought without losing their power of development. They always give rise to females.

Among the insects, parthenogenesis is exceptional; nevertheless, it commonly occurs among the aphids and the degenerate scale bugs. The female aphids produce eggs which develop in the body without fertilization, and the young are brought forth in a fairly advanced stage of development. In some species there may be several generations of parthenogenetic females. In the fall, males and females are usually produced,

Fig. 118—The black fern plant louse, winged and wingless females. (After Essig.)

and the latter give rise each to a relatively large egg which is fertilized and develops in the next spring into a female that begins another cycle.

Parthenogenesis among the bees, ants, and their allies, is associated with the determination of sex. It has long been known that the males, or drones, of the common hive bee are developed from unfertilized eggs, while the fertilized eggs develop into queens or workers. The fact has much more recently been established that there are only half as many chromosomes in the cells of the drone as there are in the cells of the other sex. The reduced number of chromosomes, however, does not occur in all forms arising by parthenogenesis. In several animals, as Weismann has shown, there is only one polar body formed in parthenogenetic eggs, the reduction division presumably being inhibited. In the eggs of the brine shrimp, Artemia, which develop parthenogenetically, the nucleus of the second polar body, instead of being extruded, sometimes goes back into the egg and unites with the egg nucleus.

In the great majority of animals in which parthenogenesis

occurs, it is not the sole method of reproduction. The males, however rarely they may appear, still have their uses. Nevertheless, there are a few cases in which the males appear to have been dispensed with entirely. That such cases are rare indicates, as Weismann contends, that giving up the usual process of sexual reproduction is a dangerous and perhaps ultimately fatal enterprise for the species. Sex being, in Weismann's view, a means of producing variability, and thus making a species plastic and adaptable, the loss of the male leaves the species unable to adjust itself to environmental changes. An exclusively parthenogenetic species, according to this view, is doomed.

There is an advantage in parthenogenetic reproduction, because, owing to the fact that all the individuals are females, the species can increase at twice the rate that would otherwise be possible. But as this advantage may be purchased too dearly, most species compromise by retaining the males for the occasional introduction of a sexual generation.

Why the eggs of some kinds of animals can develop without fertilization, whereas others cannot, is not immediately apparent. In some species in which the eggs usually require fertilization, a few of the eggs, as in the silkworm, may develop without it. Several years ago the physiologist Dr. Jacques Loeb made the brilliant discovery that the eggs of sea urchins, starfish, and some other marine animals, may be stimulated to develop without fertilization if they are placed in sea water to which are added the proper amounts of certain salts. This artificial parthenogenesis, as it is called, may be induced in several ways. Loeb found that the unfertilized egg of the frog could be caused to develop by pricking the surface with a fine needle. The eggs developed into apparently normal young frogs, the highest animals which have thus far been produced by artificial parthenogenesis. There has been some speculation upon the possibility of inducing parthenogenesis in the mammals, and even in man, but there is nothing as yet to justify the hope of success.

A widespread modification of the reproductive system is found in cases of hermaphroditism, a condition in which both

male and female sex organs occur in the same individual. This is a common phenomenon in plants, both stamens and pistils being usually found in the same flower. Among animals it does not normally occur in higher forms, but it obtains regularly in many species of worms, molluscs, and crustaceans. Hermaphroditism does not necessarily, or indeed usually, involve self-fertilization. In the earthworms there is generally cross-fertilization, the eggs of each worm being fertilized by sperms received from the other. The common land snails are hermaphrodites, and there is a mutual fertilization among them, as in the earthworms. There is self-fertilization in the tapeworms and a few other forms, but these cases are exceptional. In the tunicate Ciona, Morgan found that the eggs could not be fertilized by sperms from the same individual, a phenomenon which has its parallel in some plants which cannot be fertilized by their own pollen.

Hermaphroditism, like parthenogenesis, is a means of obtaining rapid reproduction, since every individual may produce eggs. Like parthenogenesis, it appears scattered about more or less irregularly in various groups of plants and animals. It is prone to occur in animals which are attached, or sessile, such as the barnacles, tunicates, and bryozoans, although it is by no means confined to such forms. Sometimes the same animal is at first male and then female (protandrous hermaphroditism) as in many marine worms and molluscs. Occasionally hermaphrodites may appear among forms whose sexes are usually separate, and there are many degrees of partial hermaphroditism. Even in forms in which the sexes are almost always clearly separate, as in human beings, each sex may possess small rudiments of the organs that are fully developed in the other. Under certain conditions, curious jumbles, called intersexes, are produced, whose peculiarities are of special interest in relation to the old problem of the determination of sex.

One important phase in the perpetuation of life to which the energies of animals come to be more and more directed as life advances, is the care which parents bestow in protecting and pro-

viding for their offspring. Primitive animals do not give themselves the least concern over the welfare of their progeny. The great majority of the worms, molluscs, crustaceans, to say nothing of still lower invertebrate animals, betray no active solicitude for either their eggs or young. It is true that the lower invertebrates occasionally manifest a dim suggestion of active care for eggs. The leech Clepsine carries its eggs beneath the body, and if the egg mass is slightly displaced, efforts are made to get it into a normal position. Many crustaceans carry their eggs in special brood pouches under the thorax, as in amphipods and isopods, or else attached to the appendages on the lower side of the abdomen, as in crabs, lobsters, crayfishes, and their relatives. The eggs in these forms are deposited in the brood pouches when they are laid, or else become attached by an adhesive secretion to the abdominal appendages. In either case the protection which they receive is due merely to the structural devices of the maternal body and not at all to the active efforts of the animal itself. In the amphipods the young may be carried in the brood pouch for some time after hatching, until they are sufficiently mature to shift for themselves, but the mother amphipod, far from taking any care of them, will capture and devour them as readily as any of the other small creatures upon which she preys. In studying the habits of one species, *Amphithoë longimana*, I have taken the young from the brood pouch with a fine pair of pincers and offered them to the mother, who seized and ate them without the least ceremony. It is only in a grossly material sense that the Amphithoë is fond of her offspring.

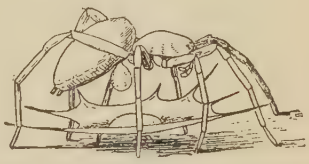

Fig. 119—Female spider Drassus, laying an egg on sheet of web. (After Emerton.)

Parental affection has had a very long evolutionary history. The beginnings of care for the next generation are to be found in the blind instinctive performances by which animals provide in a more or less mechanical fashion for the protection of their eggs or their deposition in situations which may afford food for

the young. The flesh fly deposits her eggs on decaying meat; the various species of butterflies and moths lay their eggs upon the kinds of plants suitable as food for their larvæ; dragon flies, May flies, mosquitoes, and other insects with aquatic larvæ lay their eggs either on or in the water; but none of these creatures has the least notion of why it does these things, nor does it know anything, nor in most cases has it any means of knowing anything, of the larvæ to which its eggs will give rise. Fabre has shown that the solitary wasps which take so much trouble

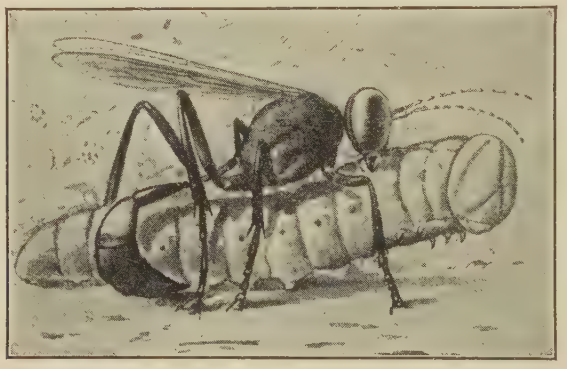

Fig. 120—The wasp *Ammophila urnaria*, stinging a large caterpillar. (After Peckham.)

in providing food for their future larvæ, do not recognize their own offspring when they see them. Normally they never do see them. The wasp, Ammophila, for instance, digs a hole in the ground and goes in search of a caterpillar with which to provision her nest. When one is found, the wasp proceeds to sting it on the ventral side of the body, inserting her sting so that the poison is injected near the ganglia of the nerve cord. She then drags her paralyzed victim to her nest, deposits an egg upon it, and carefully buries it in her hole. The larva hatching from the egg eats the caterpillar, passes through the pupa stage, and emerges as a fully developed wasp. After the mother wasp has made provision for her future larva and neatly finished the job by filling up her hole with dirt, she flies away without giving any further attention to her progeny. She is impelled by her remark-

able instinct to make elaborate provision for her offspring, which she will never see and about which she has, and can have, not the least knowledge.

Apparently care for eggs precedes care for young. Many animals take great pains to make proper receptacles for eggs, although they have no solicitude for their offspring. Spiders habitually inclose their eggs in a cocoon of web and then leave them. A somewhat exceptional case is furnished by the female of the running spider Lycosa, which incloses her eggs in a spherical cocoon which she carries about until the eggs hatch. If the cocoon is taken away from her she hunts about for it, and if one of her legs accidentally touches it she quickly seizes her treasure and carries it about as before.

FIG. 121—*Dolomedes mirabilis*, carrying her cocoon. (After Blackwall.)

The young which emerge from the cocoon are carried for a time by the mother, who seems to be little discommoded by the squirming mass of spiderlings clinging to her body. The mother, however, does not actively care for her progeny. Her parental solicitude apparently goes no further than a sort of good-natured tolerance of their presence.

In some forms the work of caring for the eggs devolves upon the male. The male sea spider is provided with special appendages by which he carries the egg masses which are received from the female at the time they are laid. The male obstetrical toad, *Alytes obstetricans*, collects the gelatinous egg strings as they pass from the female and carries them entwined about his hind legs. Another amphibian, *Rhinoderma darwinii*, retains the eggs in a pouch connected with his mouth, and a similar habit is found in the males of some species of catfish. The male seahorse carries the eggs in a pouch below his body. In several kinds of fish the males construct nests in which the females spawn; and in the stickleback and the fresh-water dogfish Amia, the males guard the nests.

Some animals remain with the eggs for a time as if to guard them. Such a habit is found in the female of the newt Desmognathus; and the python coils about its eggs, whose hatching is said to be facilitated by the warmth received from the parent's body. In almost all of the birds the eggs are objects of great solicitude and they have come to be dependent upon the heat of the bird's body for their development. Care in the birds extends also to the young until they are ready to make a living for themselves. One might be prone to think that a brooding hen has some sort of presentiment of the downy young chicks that are to be the outcome of her three weeks' devoted labor of incubation. It is much more likely, however, that she is concerned about just eggs, being led by her blind instinct to follow this particular occupation, as she is led by instinct at a later stage to brood, protect, and provide food for her little flock, all of whom have their peculiar instinct to come at her call and to cuddle for warmth and safety under her protecting wings. Parental love emerges very gradually out of the blind instinctive performances by which animals are led to make provision for their eggs and young offspring. One of its earliest manifestations is in the instinct of protection. Ants, bees, wasps, and termites are pugnacious defenders of their nests. The male of the dogfish we have mentioned swims about for a time with his brood, and he guards them against enemies, but soon the little fishes

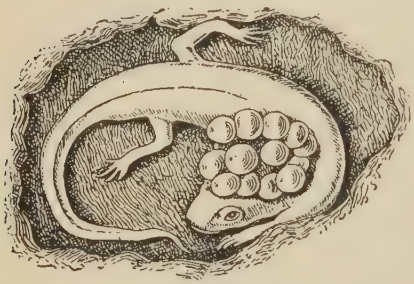

FIG. 122—The newt Desmognathus, coiling about its eggs. (After Wilder.)

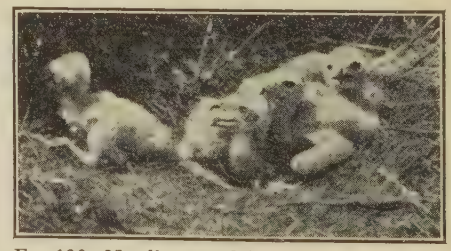

FIG. 123—Nestling marsh hawks. (After Baker.)

scatter and parental care vanishes. A mother bird, though naturally timid, will often bravely defend her young from attack; and among the mammals the mother with young is usually much more aggressive than she is under ordinary circumstances. Pugnacity toward outsiders goes along with increased solicitude for the safety of the dependent progeny, just as jealousy of rivals goes along with love of mates. Both love and animosity are woven into the conduct of animals in the interest of perpetuating their kind, and both have their uses.

Parental care in the birds comes to demand more and more of the energies of the individual as we pass from lower to higher

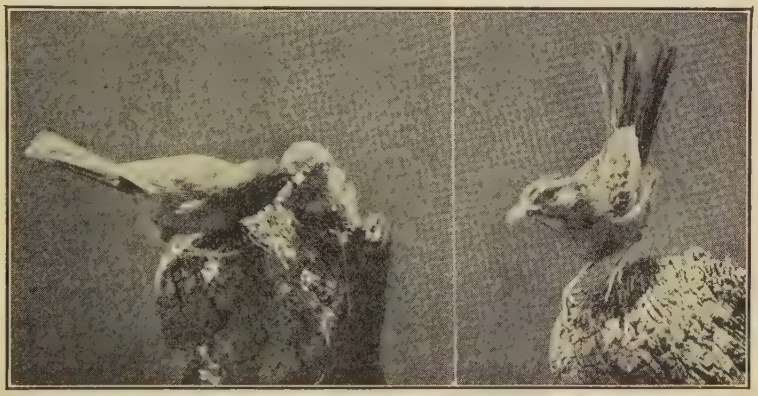

FIG. 124—Rufus crowned sparrow and young. The figure to the right shows the parent bird with food in its bill for the young. (From a photograph by J. Dixon.)

forms. The primitive birds usually lay many eggs in rather crude nests, and the young, which are hatched in an active condition, are soon able to make their own living. With the higher song birds there are often elaborately constructed nests nicely lined with soft downy feathers; few eggs are laid, and the young, which are hatched in an immature state, are tended with great care. Frequently the male and female parents take turns in feeding and protecting the young as they did in incubating the eggs. The excrement of the young, which is inclosed in a sort of membranous, gelatinous sack, is carefully removed by the parents. The period of active care is prolonged until after the

young birds are well feathered and are able to fly. Often one sees a nearly grown young robin begging food from indulgent parents who continue their ministrations after it is quite able to provide for its own wants.

An intimate association between mother and offspring is necessitated in the mammals by the circumstance that the young derive their sustenance from the mammary glands. The instinct of the young to suck, and the instinct of the mother to yield to the nutritive demands of her offspring, are correlated modes of behavior that extend throughout the whole class. As we pass from the lower to the higher mammals we find more care bestowed upon the offspring, and the period of association between parents and offspring comes to be lengthened. Among the higher mammals we meet with undeniable signs of true maternal affection. In the *Descent of Man*, Darwin remarks that "Rengger observed an American monkey (a Cebus) carefully driving away the flies which plagued her infant; Duvaucel saw a Hylobates washing the faces of her young ones in a stream. So intense is the grief of female monkeys for the loss of their young that it invariably caused the death of certain kinds kept under confinement by Brehm in N. Africa. Orphan monkeys were always adopted and carefully guarded by the other monkeys, both males and females."

Mr. John Fiske in his celebrated essay on "The Meaning of Infancy" has pointed out that the lengthening of this period of dependence affords an opportunity for the young to gain a richer and more valuable experience before embarking on the adventures of an independent career. As we pass up the scale of life, infancy becomes more prolonged; the young are born in a more helpless state; more effort is spent by parents upon their nurture, and more scope is afforded for the exercise of intelligence by the offspring in preparing for the exigencies of living. Successive generations thus become more closely tied together. At first the ties are mere blind instincts, but later they come to be those of affection manifested in the love of mates, the love of offspring, and finally a devotion to the larger social group. Gradually

the processes involved in the perpetuation of life have perfected as their final fruit the highest forms of human endeavor. But they all go to maintain the life process which, as Aristotle has remarked, has its end in itself.

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CHAPTER XI

THE DEVELOPMENT OF SOCIAL LIFE

In the preceding chapter we have considered the multifarious activities connected with the perpetuation of life, from the fission of the simplest organisms to the development of parental care and the establishment of the family. The development of social groups in animals may be regarded as a continuation of the general course of evolution that we have briefly traced. Most students of social evolution in the animal kingdom hold that societies generally arose through the gradual expansion of the family. Social aggregates of animals are found in many very distantly related groups, and it must therefore be concluded that they have had many independent origins.

Before treating of societies as they are found in the social insects and the higher birds and mammals, it will be instructive to consider briefly the colonial aggregates that occur among the lower invertebrates. Even the Protozoa, as we have seen, form colonies, and the same habit is common among sponges, hydroids, and many other groups. These aggregates of individuals are often called societies, and they exhibit many analogies with the social organizations of free individuals among higher forms, but it is perhaps best to call them merely colonies, reserving the term society for an organized group of independent animals.

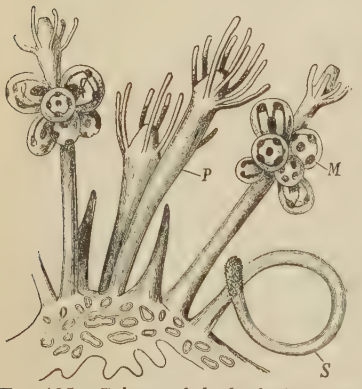

FIG. 125—Colony of the hydroid *Podocoryne carnea: P*, polyp; *M*, medusa buds; *S*, protective hydroid. (After Grobben.)

A good illustration of a colonial group is afforded by the hydroid Hydractinia which frequently grows upon the shell inhabited by a hermit crab. The colony is formed by many hydroids arising from a common branching stolon which adheres closely to the shell. In the typical hydroid individuals there are tentacles surrounding the mouth in the usual manner. These individuals are the feeding hydroids. Others lack mouth and tentacles, but are heavily armed with nettling cells. These are the protective hydroids. Still others, the reproductive hydroids, bear the sex cells. There is thus a division of labor among the individuals of the colony much as there is in human society, but in Hydractinia all the individuals are organically connected.

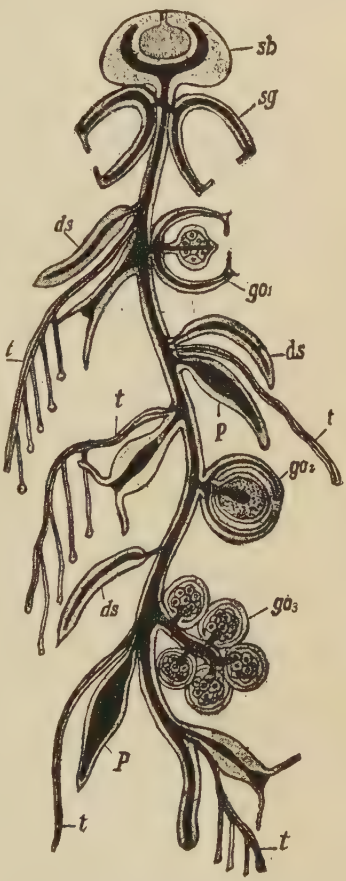

FIG. 126—Diagram of a siphonophore colony: *sb*, float; *sg*, swimming bells; *ds*, bract; *t*, *t*, tentacles; go_1, go_2, go_3, reproductive zoöids; *p*, palpon. The digestive cavity is represented in black.

One large group of the Cœlenterates, the Siphonophores, consists of aggregations of diversified individuals among which there is a well marked division of labor. Many of these denizens of the high seas are furnished with a float and a series of swimming bells which are individual medusæ specialized for the function of locomotion. There are feeding individuals, reproductive individuals, and sometimes individuals highly modified for the function of protection. The Portuguese man-of-war is one of these Siphonophore colonies, and a formidable creature it is on ac-

count of the exceedingly poisonous stinging cells on its long tentacles. In the Siphonophores the individual members show a high degree of subordination to the general aggregate, being sometimes reduced to mere organs of what appears, upon superficial acquaintance, to be a single animal with many appendages.

Fig. 127 Portuguese man-of-war. (After Agassiz.)

Animal colonies of the types we have mentioned may be said to result from the incomplete separation of individuals in the process of asexual reproduction. The individuals arising by budding remain together and become modified in different ways so as to subserve a variety of functions. As J. A. Thomson remarks, the unity of the whole "is often increased, not diminished, by the fact that the individuals are not all alike." Such groups resemble societies in that there is division of labor among the members combined with a considerable degree of mutual dependence.

Passing to animal societies in the stricter sense of the term, let us consider some of the stages of social evolution among the insects. The most complete series of transitional forms between solitary and highly social species are to be observed among the bees. Starting with an illustration of the life of a typical solitary bee we may take a species of Osmia, *O. papaveris*. The female of this species constructs a very simple nest consisting of a shallow hole in the ground which she lines, in accordance with her fastidious taste, with the petals of the poppy. Then she proceeds to store the nest with pollen and honey, and when the hole is about half filled, she deposits an egg upon her supply

of provision, fills up the remainder of the hole with dirt, and goes off to repeat the same performance several times more during the season. The young larva eats the stored food, pupates, and emerges the next year as a mature bee. During no part of her industrious life does the Osmia come into contact with her progeny. In this respect her life is like that of hundreds of other species of solitary bees.

FIG. 128—Nest of the solitary bee *Osmia papaveris*: *e*, egg; *p*, pollen.

The genus Allodape, according to the observations of Brauns, presents several transitional stages between purely solitary bees and bees which form primitive societies. These small bees make tubular nests in the dried, hollow stems of plants. Some species provision their nests once for all and leave them. Other species continue to bring food to their nests after the eggs hatch, and place it before the hungry larvæ. By a very simple step, there is thus brought about an association between the mother and her family. In still other species the mother feeds the individual larvæ, each of which has reserved for it a certain amount of space in the nest. The mother in a few cases continues to feed her young until some of the larvæ emerge as young bees. These then assist the mother in feeding the young as they make their appearance. There is consequently formed a rudimentary society of individuals coöperating in a common work.

A very interesting further stage in social evolution is found in the bumblebees. During the spring or early summer, the large queens, which are the only individuals that survive the winter, may be observed seeking some abandoned hole of a field mouse, or other cavity in which to make their nest. Having selected a suitable cavity the queen proceeds to line it with bits of grass or moss. Then she begins to construct a cell which is made from the wax scales secreted beneath her own body. After storing a cell with a mixture of pollen and honey commonly known as bee bread, she lays a few eggs within it and seals it over. She

also constructs a somewhat similar cell which she fills with honey as a sort of reserve food supply. Much of her time is now spent in sitting upon her cell, the hatching of the contained eggs being hastened by the warmth of her body. The eggs hatch in a few days, and the queen adds more food which she injects into the cell after making a hole in the top with her mandibles. When the larvæ attain their growth they spin a cocoon about themselves and pass into a pupa stage from which they emerge as young females. Many of these are relatively small, especially if they received a scant supply of food in the larval state. These smaller females constitute a worker caste, although there is no sharp line of demarcation, such as there is in the honeybees, between the workers and queen. The new brood of workers bring honey to the nest, build new cells of wax, and occupy themselves with providing for the larvæ. The original queen henceforth devotes herself more and more to the function of egg-laying, and rarely leaves the nest. Later in the season some of the younger females also lay eggs which, being unfertilized, develop into males, or drones. The larger females, or queens, are impregnated, and these leave the nest while the rest of the colony perishes with the advent of cold weather. The young queens winter over in protected nooks and start new colonies in the following spring.

The whole society among the bumblebees consists of one or more generations of the progeny of a single mother. With the growth of the colony there soon comes to be a division of labor between the queen and her daughters, and although the development of the latter may be inhibited until it results in sterility, the faithful virgins throw themselves with entire devotion into the work of providing food, tending the larvæ, and protecting the nest against invaders.

Among the bees belonging to the large subfamily Meliponæ, the colonies, which sometimes include as many as 80,000 individuals, consist of clearly defined castes of workers and queens, together with occasional males. The young are reared in waxen cells which are closely packed, side by side, in layers within a

nest commonly located in a hollow tree or in the ground. In some species the queens are reared in cells of larger size. New colonies are founded by young queens that leave the old nest, accompanied by small numbers of workers. With the appearance of the new brood, the workers take over most of the household duties, collect pollen and honey, while the queen becomes more and more sluggish and finally devotes herself solely to laying eggs.

The acme of social evolution among the bees is attained by the common hive bee. The queen no longer starts the nest, nor does she take any part in the household duties of the group. After her nuptial flight, when she is fertilized by a drone and receives a store of spermatozoa which she may retain for years, she settles down to a routine of egg-laying. The queen has lost several structures and instincts which the queens of more primitive species possess. She has no wax glands, wax pincers, or pollen basket, but all these structures are retained by the worker caste. Her tongue is shortened, and her brain is smaller than that of the workers. In most features, except the development of her ovaries, she is a degenerate. The males, unlike those of some of the more primitive bees, which coöperate in the work of the family group, become idle pensioners upon the industry of the workers, and, after the mating period is over, when the opportunity for performing their one social service is past, they are mercilessly attacked by the workers and stung to death.

Normally, the hive bees make their abode in the trunk of a hollow tree. Their honeycomb consists of a double layer of hexagonal cells of wax which lie horizontally on either side of a central plate. The cells are of three kinds: (1) the ordinary cells which serve for the storage of honey or the rearing of larvæ; (2) the somewhat larger drone cells; and (3) the queen cells which are much larger and more irregular in form than the other two types. The differences between queens and workers are the result of feeding. The larvæ fed upon an ordinary plain diet of pollen and honey develop into workers; those which

are fed largely upon a product of the salivary glands, known as royal jelly, become queens. If a queen dies or disappears, and there are no others about to emerge, the workers are said to construct a larger cell and to feed its occupant upon royal jelly, thereby converting it into a queen.

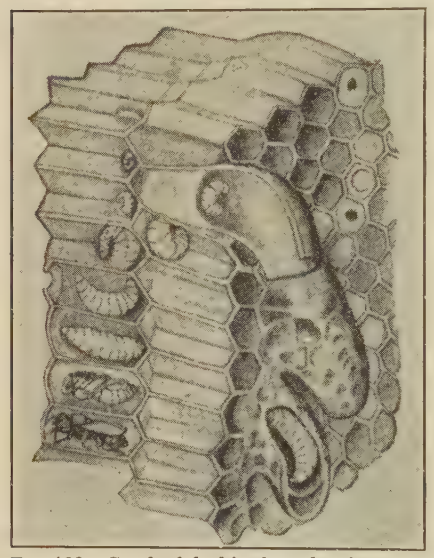

FIG. 129—Comb of the hive bee, showing eggs, larvæ, pupæ, and large queen cells. (After Benton.)

The life of the hive-bee community is a continuous one, since it may outlast the life of many queens and numerous generations of workers. When the community becomes too populous, the old queen and a part of her retinue of workers leave their old home, or swarm, as the bee keepers say, while the old colony continues to operate under a new queen. To a large extent, the bee community consists of the progeny of one mother, but it includes somewhat more than a single large family. Nevertheless, it is clearly the outgrowth of a single family in the strict sense of the term.

FIG. 130—Castes of the hive bee: *A*, drone; *B*, queen; *C*, worker. (After Benton. Courtesy Blakiston's Son & Co.)

Owing to the evolution of the bee state there has been a division of labor between the workers and the queen, the two

castes combined performing the work of the females of the primitive solitary, or incipiently social species. The reproductive functions of the pre-social ancestor have been retained by the queen, while the instincts for gathering food and taking care of the household have been bequeathed to the workers. Queens and workers have divided between them the original endowments of their ancient maternal ancestor, but they have added to them at the same time, because the instincts of the hive bee are the most elaborate and specialized that are found in the bee family. The workers are, in one sense, imperfectly developed females, the difference between worker and queen being determined by the food given to the young larva. The meager allowance meted out to the workers inhibits the development of their ovaries, while the royal jelly fed to the queen stimulates the development of the reproductive functions, and at the same time inhibits the development of many structures and instincts that characterize the worker caste. Queens and workers are therefore complementary beings, each having developed certain features of a common inheritance that are suppressed in the other. The queen nevertheless transmits the inheritance of both, and also the qualities of the drone, which is a very different creature from either of the other castes. As previously stated, the drones arise from eggs which develop without being fertilized.

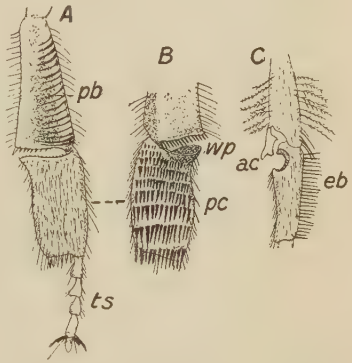

FIG. 131—Legs of the worker hive bee: *A*, lower part of third leg seen from the outside; *pb*, pollen basket; *ts*, tarsus. *B*, inner face of metatarsal joint, showing the pollen comb, *pc*, and the wax pincers, *wp*. *C*, part of first leg; *ac*, antenna cleaner; *eb*, eye brush.

The wasps, like the bees, have both solitary and social species, and they also present several transitional stages from the one to the other. We are compelled to omit any description of the instinctive behavior of the solitary wasps, beyond the short

account given in the previous chapter, and must refer the student to the works of Fabre and the Peckhams for an adequate account of these fascinating insects. Some of the primitive social wasps show merely a rudimentary social life, or perhaps we should call it family life, because of the fact that the female, instead of supplying her nest once for all with food, continues to bring new material for the growing larvæ. A more advanced stage is shown by the common genus Polistes. These wasps make cells out of a

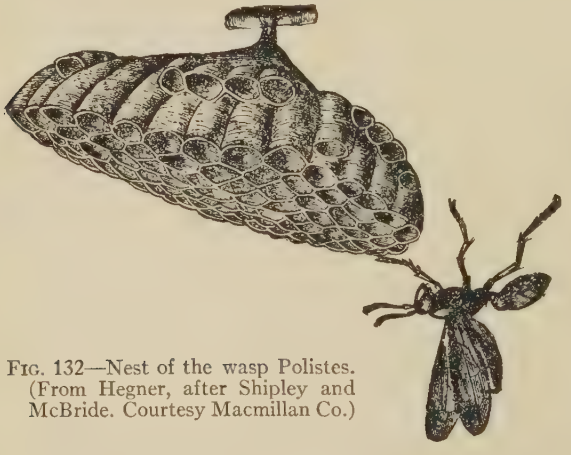

Fig. 132—Nest of the wasp Polistes. (From Hegner, after Shipley and McBride. Courtesy Macmillan Co.)

sort of paper which is formed of chewed-up fibers of wood fastened together by a secretion of the salivary glands. The cells are arranged side by side to form a plate, or comb, which is suspended by a stalk attached near the middle of the upper side, the cells being open at the lower end. A small amount of food in the form of paralyzed insects or spiders is deposited along with one or more eggs in each cell. The colony is started by a single queen, but her offspring, which at first are mostly small females, or workers, coöperate in building more cells and in supplying them with provisions. Later in the season, males are produced which fertilize the more perfectly developed females, or queens, and the latter, like the queen bumblebees, winter over and start new nests in the spring.

The more familiar yellow jackets and hornets generally form

larger communities than the Polistes, and their nests are composed usually of several plates of comb arranged in a vertical series, the whole being surrounded by a paper envelope with an entrance at the bottom. Sometimes the nests are suspended from the branch of a tree, or they may be built in the ground. They are started by a single female who constructs at first a small nest much like that of Polistes, but the workers that first emerge help to enlarge the nest, which by the end of the summer may contain several thousand individuals. The whole society is nevertheless the progeny, directly or indirectly, of a single mother, or, in other words, a greatly enlarged family.

FIG. 133—Nest of the yellow jacket, *Vespa diabolica*, cut open through the middle, showing tiers of comb and several layers of the paperlike covering. (From a photograph by Herms.)

FIG. 134—Two yellow jackets, *Vespa diabolica*. (From a photograph by Herms.)

By far the largest of all the groups of social insects, both in the number of species, which exceed 3500, and in individuals, which are as the sands of the sea for multitude, are the ants. All of the ants are social, but there are many gradations in

the development of community life from the primitive ponerine ants to the highly organized social groups. With the exception of some species that live within the hollow stems of plants, the ants dwell in galleries excavated under the ground or in the rotten wood of stumps or fallen trees. In the galleries, certain parts may be set aside for rearing larvæ, and others for the storage of

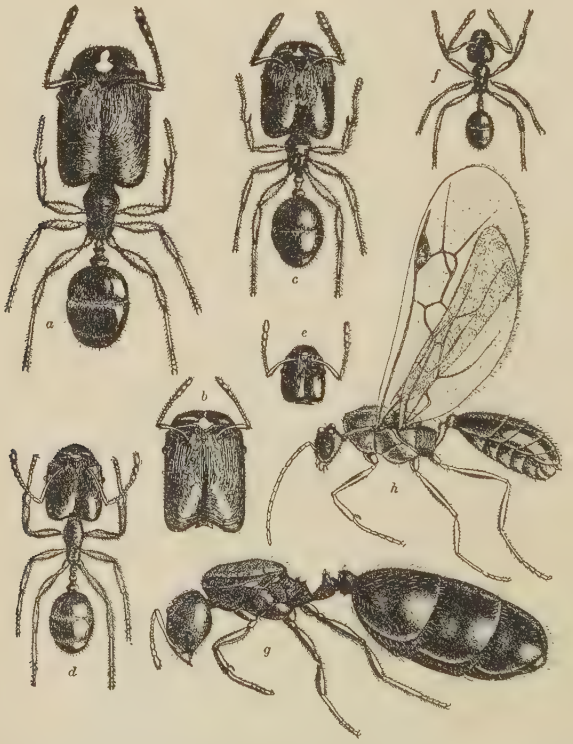

FIG. 135—Various castes of ants (*Phcidole instabilis*): *a*, soldier; *b-e*, intermediate workers; *f*, typical worker of the small class; *g*, female after shedding her wings; *h*, male. (After Wheeler. Courtesy Columbia University Press.)

food, but the arrangements are frequently modified in relation to variations in moisture, temperature, and the size of the colony.

There are commonly three distinct castes, males, females, and workers, and frequently the workers are of two or more distinct

types. There is often a large worker caste with big heads and strong jaws—the so-called soldiers. These ants function in the defense of the colony, while the smaller workers excavate galleries, collect food, and take care of the eggs and young larvæ. The more highly developed communities may persist for many years, outlasting the lifetime of several successive queens. A colony may, therefore, continue to grow for a long time and may finally include several hundred thousand inhabitants. Such communities frequently have several queens. As among the hive bees, the queen is fecundated only once; the spermatozoa derived from the male are stored in her spermatheca and retain for years the potency of fertilizing the eggs. Queen ants have been known to live for over fifteen years, which is a ripe old age for an insect, especially since so many insects seldom last longer than a single season.

New nests are established in several ways among ants, but they are usually started by a single queen. In the sunny days of spring or summer, ants may sometimes be seen to swarm. This is a time of great excitement in the ant world. Winged males and females emerge from their subterranean galleries and fly into the air, where mating takes place as among the social bees. Each impregnated female alights and seeks some protected nook, or digs a small hole in the ground. She soon rids herself of her wings, of which she will henceforth have no need, and proceeds to close up the opening of her abode. She now waits for her eggs to mature. The large wing muscles are broken down and utilized as food for the growing eggs. When the latter are laid and hatched, the larvæ are fed from the mother's saliva. The first brood is constituted of small workers who enlarge the nest, take care of their younger sisters as they come along, and bring in food for the support of the colony. The queen then gives herself over to her reproductive functions, which she continues to perform as the colony enlarges. The ant community which develops in this manner is thus the large family of a single queen. In some species several workers may associate themselves with the queen in founding a new colony, but the foregoing is doubt-

less the primitive method from which the other varieties of colony formation have been derived.

Since the larvæ of ants are soft, helpless, legless grubs, as dependent upon others of their kind as are human infants at birth, they must be assiduously fed and cared for by the workers, else the colony would soon perish. Although the workers are sterile, except for the occasional laying of unfertilized eggs, they fortunately possess a liberal endowment of maternal instincts. The life of the worker is one of unselfish service to her group. Her proverbial industry, which provoked the well known comments of Solomon, is a very important social asset, even if it is not always wisely directed. Beyond obtaining the small amount of food required for her personal needs, she concerns herself relatively little with her own private aims; she is a creature of blind altruistic devotion to her kind. She is soldier, police officer, excavator, caterer, housekeeper, and nursemaid all in one, and in some species she may perform the additional social services of agricultural labor and kidnaping.

Ants not only supply their larvæ and queen with food, but habitually feed each other. One of the common amenities of their social life is to offer their companions some of the regurgitated contents of their crop. This partially digested food frequently contains sugar, since ants often feed upon nectar and the sweetish exudation, or honeydew, produced by aphids, or plant lice. Ants have been observed to protect aphids (their so-called cows) and to carry them at times to favorable places for securing food. The food habits of ants are exceedingly varied and sometimes eccentric. Some species are mainly carnivorous; others are chiefly vegetarians, while several kinds appear to be quite omnivorous. The discovery of a supply of food by one or more ants commonly results in bringing a whole army to the spot to profit by the find. Much study has been devoted to the powers of communication which ants possess, and it has been shown that ants follow the track of the individual that has been successful in discovering food. When ants meet and stroke each other with their antennæ, or feelers, it is perhaps too much to

conclude that they are carrying on a conversation, but the encounter nevertheless induces the one ant to follow the footsteps of its fortunate comrade. This so-called power of communication is obviously a very valuable trait for a group of social insects to possess, because it enables all the individuals to profit by the discoveries of any one member.

One of the most striking developments in the social life of ants is the institution of so-called slavery. There are many interesting variations of the slave-making habit, and various degrees of degeneracy are met with as a result of the long continued dependence of the master caste upon its slaves. A well known case, which has as yet entailed little or no degeneracy, is afforded by the widespread reddish ant, *Formica sanguinea*. Many colonies of this species are entirely devoid of slaves; other colonies include varying numbers of the smaller *Formica fusca*, or sometimes other related species. The *sanguineas* are warlike ants, and they frequently sally forth and attack the neighboring nests of the species they enslave. The adult *fuscas* that do not discreetly retire are usually killed, but their larvæ and pupæ, although eaten to a certain extent, are mostly carried back to the nest of the victors, where they are raised. The young *fuscas* take part in the household duties of their adopted home with entire loyalty to the community of their captors. The slave-makers profit by these kidnaping raids in obtaining workers, but they are quite able to get along without such forcibly imported labor; and, according to Wheeler, one variety of *Formica sanguinea* does not make slaves at all.

The large Amazon ant, *Polyergus rufescens*, has long served as an illustration of the degenerating influence of the slave-making habit. The Amazons make their periodic forays against neighboring *fuscas*, whose larvæ and pupæ they carry back to their own nests. They are well adapted for fighting, but as Lord Avebury has remarked, they "present a striking lesson of the degrading effects of slavery, for these ants have become entirely dependent on their slaves. Even their bodily structure has undergone a change: the mandibles have lost their teeth, and have become

mere nippers, deadly weapons indeed, but useless except in war. They have lost the greater part of their instincts: their art, that is, the power of building; their domestic habits, for they show no care for their young, all this being done by the slaves; their industry—they take no part in providing the daily supplies; if the colony changes the situation of its nest the masters are all carried by the slaves on their backs to the new one; nay, they have even lost the habit of feeding. Huber placed thirty of them with some larvæ and pupæ and a supply of honey in a box. 'At first,' he says, 'they appeared to pay some attention to the larvæ; they carried them here and there, but presently replaced them. More than one-half of the Amazons died of hunger in less than two days. They had not even traced out a dwelling, and the few ants still in existence were languid and without strength. I commiserated their condition, and gave them one of their black companions. This individual, unassisted, established order, formed a chamber in the earth, gathered together the larvæ, extricated several young ants that were ready to quit the condition of pupæ, and preserved the life of the remaining Amazons.'"

About the last stage in degeneracy due to dependence on other ants is presented by the species of Anergates. Only queens and males occur in this genus, the worker caste apparently having been lost as the result of parasitic habits. The males are exceptional in being wingless, and the females, although at first winged and active, soon lose their wings and become very sluggish on account of the enormous growth of the abdomen that accompanies the maturing of the eggs. Anergates lives together with ants of the genus Tetramorium and is entirely dependent upon the latter for support.

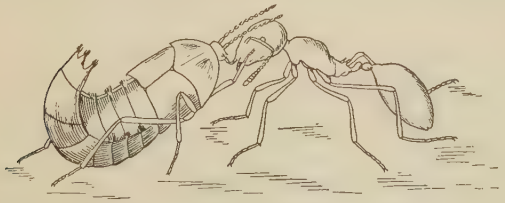

Fig. 136—A beetle *Atemeles emarginatus* being fed by an ant, *Myrmica scabrinodis*. (After Wasmann.)

We have been able to touch upon only a few of the striking social phenonema exhibited by ants, and we can only mention

the remarkable associations found between ants and the numerous guests, parasites, and commensals that occur in their nests. More than 2000 species of these myrmecophiles (ant lovers) are known, and, as Wheeler remarks, they "include not only members of nearly all the different orders of insects, but also, many spiders, mites, millipeds, and land crustaceans—creatures, which have been induced to live in more or less intimate and maleficent relations with the ants by the obvious advantages of the association."

In another large group of social insects, the termites, or white ants, as they are popularly called (although they are not ants and are frequently not white), we meet with an elaborate development of social life which affords many striking parallels with that of the true ants. The termites are primitive insects, very distantly related to the forms we have been considering. Like the ants, they are mainly subterranean in their habits, although many species build nests above ground and some live mainly in burrows excavated in wood. Their castes may be even more numerous than those of ants. The perfect males and females are winged like those of the ants, and they also break off their wings soon after they swarm out of the parental nest. In addition to the typical males and females there are, in some species, less

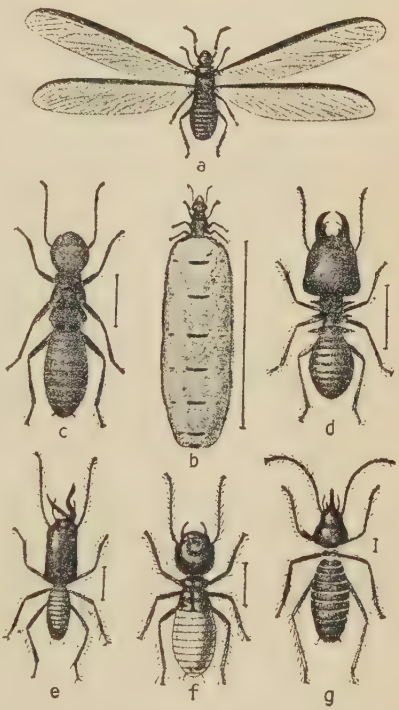

FIG. 137—Castes of termites: *a*, young female of *Termes spinosus; b*, mature female of *Termes gilvus; c*, male of Hodotermes after shedding the wings; *d*, soldier of *Termes spinosus; e*, soldier of *Termes speciosus; f*, worker of Hodotermes; *g*, one of the nasuti of Eutermes. (From Escherich.)

fully developed reproductive castes of both sexes, with or without rudimentary wings. The worker caste, which is normally sterile, consists of relatively small, wingless individuals that do most of the work of the community. In many species there is a soldier caste with large heads and very strong jaws. The soldiers exhibit little industry in the ordinary domestic affairs of the colony, but they take an active part in the defense of the nest if it is disturbed. A few species have a curious caste of small individuals called nasuti because their pear-shaped head is drawn out in front into a sort of snout. The nasuti have small and weak jaws, and there has been some uncertainty as to what function these apparently futile creatures might perform in the life of the social group. At the end of the snout there is discharged a secretion which in some forms is adhesive and which in several species appears to have an irritating effect. By virtue of this secretion the nasuti are enabled to carry on a kind of chemical warfare against invading ants, which are the worst enemies of the termite society. The nasuti often put the ants to rout, and for this reason they play a very useful part in the defense of the colony.

The various castes of workers, soldiers, nasuti, etc., unlike those of the ants, consist of members of both sexes. All these forms arise from eggs laid by the perfect insects, but it is not established that the differences between them are produced by feeding, and there is some evidence that they are due to differences among the fertilized eggs. The termites have a swarming period much like that of the ants; the winged males and females leave the nest and fly in the air, but they do not mate there. Mating occurs only after the sexes alight. The males and females, both of which soon shed their wings, associate in pairs and proceed to excavate a nest in some suitable place. Like a young married couple, the young king and queen live together in their new habitation and proceed to bring up their family. The worker termites, that first emerge from the fertilized eggs of the queen, actively aid in the enlargement of the habitation and in providing food for the king, queen, and young. As the colony

gets older and larger, the queen becomes more inactive. In some species her abdomen swells enormously so that she may become more than 20,000 times as large as one of the workers. She is fed by a throng of busy attendants; and others are kept equally busy carrying away her eggs and depositing them in suitable chambers in the nest. Escherich finds that the queen of an Indian species of Termes lays as many as 30,000 eggs in a day—a record for fecundity scarcely equaled by any other insect.

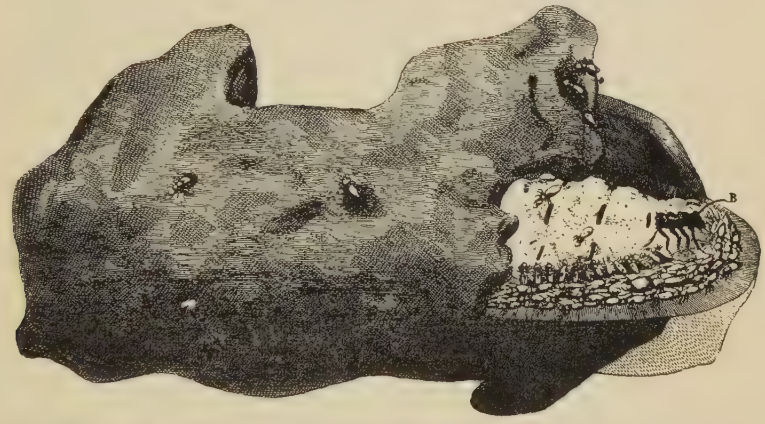

FIG. 138—A large female termite partly exposed by breaking the royal chamber, the anterior part of her body being shown at *B*. A large number of worker termites surround her. (After Smeathman.)

The queen bee or ant may be more or less degenerate on account of her reproductive specialization, but the queen termite is reduced to a mere passive instrument for the production of eggs.

One of the chief sources of food for termites is wood, and it is partly on this account that these insects become such pests in the tropics, where they destroy houses, furniture, bridges, and all kinds of wooden structures. The members of the colony continually feed each other on saliva, regurgitated food, or the contents of their intestines. Their bodies also exude a secretion which is licked off by their comrades with apparent relish. These secretions are produced to a greater extent by the queens than by the other castes, and they constitute some degree of recompense to the workers for their various services devoted to royalty.

When we consider that termites and ants belong to groups of insects that are very distantly related, it is remarkable that their social life should present so many and such striking points of similarity. There is a general resemblance in their habitations, and a parallel development of a neuter caste which frequently includes both workers and soldiers. There is a similar specialization of queens in relation to reproduction, and similar methods of mutual feeding, and of caring for eggs and young. Both ants and termites found new colonies in much the same manner after the swarming period; in both groups the males and females soon divest themselves of their wings, the workers and soldiers in both being wingless. In the nests of both ants and termites there are hordes of guests, commensals, parasites, and other creatures, and some of the termites, like some species of ants, cultivate underground gardens of fungi upon which they feed. As Wheeler has remarked, these parallel developments of culture may not be without interest to the anthropologist in his study of the possible independent origin of different institutions in man.

Social life as it appears in higher animals such as birds and mammals is quite different from that of the insects. There are no distinct castes, and there is comparatively little division of labor between different members of the social group. Most of the birds and mammals that form associations are properly described as gregarious. Watch a flock of domestic geese or ducks and you will see with what tenacity the group keeps together; when one turns about all turn; when one flees, all follow; and they all commonly utter their cries in concert. If we succeed in isolating an individual from the flock the creature is obviously uncomfortable and makes every effort to rejoin its comrades. Many birds form associations only while they are migrating, but others are permanently social. Birds of prey sometimes unite in an attack, and smaller birds may combine to ward off a common enemy. According to several observers, cranes place sentinels on the outskirts of the flock to warn the others of danger during the periods of feeding. Brehm says of parrots that "they post sentries to keep watch over the safety

of the whole band, and they are attentive to their warnings. In case of danger, all take to flight, mutually supporting each other, and all simultaneously return to their resting place. In a word, they always live closely united."

To a certain extent, the associations of birds are brought about by the tendency to seek common localities for breeding, feeding, or protection. This tendency has been the occasion for the development of instincts for self-defense against the encroachments of their own kind. The insect society, on the other hand, is communistic. All the members have the same interest in the young, the construction of their common habitation, and in the defense of the group; and on account of the widespread custom of mutual feeding even the nutrition of the individual has come to be largely a general social activity. But the birds that form social groups retain their individual interests in their own nests and young.

Much light has recently been thrown on the social behavior of birds through the studies of Howard. During the migration of birds into their breeding areas the males usually precede the females. The males in a great many species take up their stations in a given locality and occupy an area of greater or less size according to the species. These areas are resolutely defended against invaders. Frequent fights ensue as a result of the invasion of a territory by other males. The male exercises a sort of proprietary right over the region which he preëmpts. Invading birds are attacked and driven away, but once the intruder is expelled beyond the boundary of the area, the hostility of the owner ceases.

With the arrival of the females there develops a rivalry among the males who attempt to lure their prospective mates through the power of song and the ceremonies of courtship to enter the bonds of domestic life, and share the occupancy of their area. The search for food in order to supply the young is normally confined to the territory belonging to the family. There are often neutral grounds within which the birds mingle in perfectly friendly relations, and after the breeding season is over the tend-

ency to resent the trespassing of neighbors becomes weakened. As Howard remarks, "the outstanding feature of bird life in the winter is sociability; that of the spring is hostility."

The instinct to preëmpt territory that provides sufficient food for the support of the family is an instinct in the service of reproduction. A large part of the fighting which goes on among birds is the result of efforts to protect territory from invasion. The attitude of a bird in relation to its fellows is often completely changed after it has established itself in a particular locality. Its behavior is a part of the process of perpetuating life, using this term in the wider sense of including care for the welfare of progeny.

The mammals have developed social groups of many kinds. The common prairie-dogs of our western plains cluster together in their so-called villages in which individuals appear to interest each other by their chatter and play. While sitting upright near their holes a danger signal from one of the individuals makes the whole group disappear in an instant. Even among mammals which are relatively solitary, such as the rabbits, the sight of one individual in flight affords the occasion for a similar flight among the others. Warning cries are common among mammals as among the birds, and cries of distress often bring other individuals to the spot.

Horses, sheep, cattle, and antelope, frequently associate in herds which afford a means of defense against the larger carnivores. Kropotkin in his book on *Mutual Aid a Factor in Evolution* says of wild horses: "When a beast of prey approaches them several studs unite at once; they repulse the beast and sometimes chase it; and neither the wolf nor the bear, not even the lion, can capture a horse or even a zebra as long as they are not detached from the herd." Wild cattle when attacked often huddle together into a compact group with the cows and calves in the middle and the bulls on the outside facing the enemy. Galton, speaking of the oxen of South Africa, says that "although the ox has so little affection for, or individual interest in, his fellows, he cannot endure even a momentary severance

from his herd. If he be separated from it by stratagem or force he exhibits every sign of mental agony; he strives with all his might to get back again, and when he succeeds he plunges into its middle to bathe his body with the comfort of closest companionship."

Societies in mammals are formed for offense as well as defense. Wolves, jackals, and hyenas hunt in packs, and are thus able to prey upon animals too large for a single individual to overcome. The beavers, on the other hand, form a sort of industrial society, since many of these animals coöperate in the construction of their dams. Among the apes and monkeys, social groups are formed partly for defense and partly on account of various other mutual services. The Hamadryas baboons, according to Darwin, "turn over stones to find insects, etc., and when they come to a large one as many as can stand around, turn it over and share the booty." Brehm tells of a group of baboons all of which had been driven off by a pack of dogs with the exception of a young baboon about six months old which was calling loudly for help. One of the largest of the males, "a true hero," came back, seized the young baboon from the midst of the astonished dogs and brought it safely away. Although some species are generally solitary in their habits, many kinds of the apes and monkeys form bands under the leadership of a large male. These bands are held together by strong mutual sympathy, and there are many accounts of gratuitous services performed by one member for another. Apes and monkeys derive much satisfaction from association with their kind, and are unhappy when isolated.

Among the higher animals societies are not merely large families as they usually are among the insects. Nevertheless, social life depends upon instincts which are primarily of service in the maintenance of the domestic group. The affection of parents for their young, which often lasts until the latter are nearly grown, the instinct of parents to defend the young when they are in danger, the response to calls by both parents and offspring, and the services of parents to each other in the interest of the family group—all these traits afford an instinctive basis of aid

to others which is readily extended to members of the species beyond the limits of the immediate family. Animals respond to a cry of distress from one of their fellows because they are by nature responsive to such cries on the part of their young and mates. The family is the nursery of the altruistic instincts upon which social life is founded. The reason why societies have been formed along many independent lines in both birds and mammals is because societies are the product of an easy transition on account of the foundations for social life that are laid in the family.

Societies among the lower animals, as well as among human beings, are mutual benefit organizations. They are devices, so to speak, for enabling the species to get on. In this respect they are like the family. In the previous chapter we have seen how the perpetuation of life has come to involve the evolution of parental care. We are now prepared to appreciate the fact that social evolution also is a continuation of essentially the same line of development. Society requires mutual aid, often the sacrifice of self, but Nature, to speak figuratively, is not so much interested in the individual as she is in the preservation of the stock. The worker hive bee often loses her life when she stings an enemy, because the sting cannot be withdrawn from the flesh. She is but a pawn in Nature's game to be sacrificed, if need be, for the larger interests of the social group.

Wherever social life develops among animals it tends to emphasize certain traits of behavior. One of these is pugnacity. In most of the solitary insects this trait is conspicuous by its absence. One cannot elicit the least exhibition of anger from grasshoppers, flies, or moths, but the case is very different when one is dealing with yellow jackets or hornets. Every boy knows that a nest of bumblebees is not to be molested without due precautions. Stir up a nest of ants and the occupants swarm out ready for an attack. Not only do they defend the nest against intruders, but many kinds engage more or less regularly in warfare against other ants. The driver ants sally forth in long columns attacking almost every living creature that comes in

their way. Many kinds of ants treat as an enemy any individual of their own species not belonging to their immediate social group. Students of ant life have discovered that whether an ant is received as a friend or an enemy depends mainly upon its odor, and Bethe found that two groups of hostile ants could be made friendly if they were thoroughly shaken together in a bag so that each kind would take on the odors of the other. A striking indication of the importance of fighting among ants is furnished by the frequent occurrence of a special warrior caste with large jaws especially adapted for attack.

Passing to the remotely related group of termites almost at the lower end of the insect series, we again meet with conspicuous manifestations of the fighting instinct. Here again we find a distinct soldier caste which is especially active in repelling attacks. Smeathman in speaking of the warriors of an African species says: "They attacked fiercely any intruding object and as fast as their front ranks were destroyed others filled up their places. When the jaws closed in the flesh, they suffered themselves to be torn into pieces rather than loosen their hold." The unbounded fury exhibited by some species when their habitation is disturbed affords a most amusing spectacle—providing the observer keeps at a safe distance.

In the social groups of birds and mammals it is common to find that the members are readily aroused to anger by attacks upon one of their kind. Collective pugnacity is an important asset in preserving the integrity of the social group and consequently in insuring the safety of its component individuals. Man, who is a social animal, appears to be quite as liberally endowed with the fighting instinct as the lower mammals are, and much more so than most of the nonsocial species. Being a social animal, he is willing to fight not only for his own rights, but for those of his fellows. Throughout his history, he has engaged in conflict, and he has found his greatest glory in this occupation. Civilization may eventually tame him down, but it will require much wise endeavor to subdue his instinctive pugnacity, or direct it into useful channels.

Another set of tendencies fostered by social life, and one which is seemingly the reverse of the trait just described, consists of the instincts which prompt animals to work in the service of their fellows. Mutual aid in animals, as Kropotkin has shown, is both widespread and important.[1] In the higher animals it is prompted by affection and social sympathy, which comes to be more highly developed as life advances. Among the social insects mutual aid rests to a greater extent upon a basis of blind instinct, but it frequently involves greater sacrifices of the individual to the general weal. A measure of altruism is everywhere an essential condition for the maintenance of a society. It commonly stops with the limits of the social group, or at least the species. And even man himself exhibits a sympathy with his fellows which frequently does not extend beyond the limits of his tribe or nation.

When we study the relation of pugnacity and mutual aid in animals it becomes apparent that these traits are not opposed, but correlative phenomena. The relation between pugnacity and affection is frequently seen in the rudimentary society of the domestic group. A female white rat kept in captivity may ordinarily be quite gentle, but when she has young she is apt to become aggressively pugnacious. Her loyalty to her own goes along with hostility to all other creatures that may possibly be a menace to her offspring. In human beings we find much the same combination of aggressive and altruistic traits that is displayed by the higher mammals. The qualities which we share in common with our nearest animal relatives are the basis of both our good and evil actions. Our fighting propensities and the impulses that lead us to be helpful to our fellows have played an important part in the development of organized society, as they have in the development of infra-human life. The proper adjustment of these apparently contrary impulses of our nature presents one of our most trying problems. There is a legitimate scope for our instinctive pugnacity, if it is only subor-

[1] Striking illustrations of mutual aid and social sympathy are furnished in Prof. W. Köhler's instructive volume, *The Mentality of Apes* (N. Y., Harcourt, Brace, 1925).

dinated to worthy ends, but the trait is a fertile source of troubles ranging from the petty squabbles of the nursery to the greatest of international conflicts. Children as they grow up gradually learn to adjust their differences in a peaceful manner, and there is perhaps more or less ground for hope that, under the influence of wise and beneficent statesmanship, nations may sometime learn to do the same.

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CHAPTER XII

COMMENSALISM, SYMBIOSIS, PARASITISM, AND OTHER FORMS OF ASSOCIATION

The associations we have thus far traced depend upon community of blood. But organisms enter into relationships of various kinds with other species besides their own. A very important part of the environment of every organism consists of other organisms. Different species in their efforts to get on in the world have had to adapt themselves to each other, and these adaptations have often entailed far-reaching modifications of structure and habit.

In the kind of association known as commensalism, organisms take up the same abode, or one may live upon or within the other, without either one living at the other's expense. There are many kinds of worms, crustaceans, and other animals that live within the cavities of sponges, receiving there protection and such food as they can abstract from the water. Certain species of small fishes live within the digestive cavity of the large sea-anemone Discosoma, and probably take advantage of some of the food captured by their protector. There are other little fishes that swim about among the stinging tentacles of the Portuguese man-of-war. A common illustration of a commensal, or messmate, is furnished by the little crab Pinnotheres which lives within the shells of oysters, mussels, and other bivalved molluscs. The crab is not parasitic upon the molluscs, although it may deprive its host of some of its food. A more

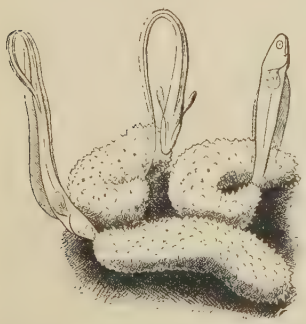

FIG. 139—*Fierasfer acus* in the act of entering the intestine of a holothurian. (After Grassi.)

curious case of commensalism is that of the female of the crab *Hapalocarcinus marsupialis* which takes up its abode upon a coral, and eventually comes to be almost surrounded by a limy inclosure secreted by the coral polyps. The crab being thus made a prisoner subsists upon the food drawn in by the action of her appendages. Another singular domicile is chosen by the small fish Fierasfer which inhabits the terminal part of the intestine of a sea cucumber. The form of the fish, which is long and narrow, is especially adapted to its environment. The tail is narrow and tapering, which is a very unusual form for the tail of a fish, but it is obviously correlated with the creature's custom of entering its habitat tail first.

There are several animals that attach themselves, temporarily or permanently, to others, but without inflicting any injury upon their benefactors. The remora has a peculiar adhesive disc on the top of its head whereby it attaches itself to a larger fish or the bottom of a boat, and thereby secures transportation without efforts of its own. The whale barnacle Coronula is always found attached to whales, and may become partly overgrown by the skin. Another barnacle, Tubicinella, lives almost completely inclosed by the whale's skin. The chief advantages gained by the barnacles probably consist in the greater amount of food secured on account of the whale's movements.

Cases of symbiosis, or associations in which each species derives some advantage from the other, are very common. Not improbably the association of the hermit crab Pagurus with the anemone Adamsia is a case in point. The anemone attaches itself to the coiled shell which is occupied by the crab, and derives the advantage of being carried about from place to place. The crab probably enjoys a certain amount of protection on account of the stinging cells of the anemone. If the anemone is removed, the crab hunts about for a new anemone which it endeavors to tear loose and place upon its shell. Another kind of hermit crab carries an anemone attached to the surface of its larger pincer. Apparently the crab makes active efforts to place an anemone in this position, for, after molting the skin, the crab tears off

the anemone from its discarded covering, places it upon its pincer, and carries it about as before.

The association of ants and aphids are in several cases symbiotic. The eggs of the corn-root aphids are protected in ants' nests during the winter and then carried to appropriate plants in the spring. The ants profit from the arrangement by deriving the sweet honeydew from the aphids. Among the numerous species of creatures inhabiting the nests of ants and termites there are many that supply their hosts with exudations secreted by various glands, and receive in turn food which their hosts regurgitate or otherwise provide.

Many kinds of Protozoa, hydroids, corals, anemones, and worms, form symbiotic associations with unicellular green algæ. The green Hydra (*H. viridis*) differs from the common brown species (*H. fusca*) in harboring minute algæ in the cells of the entoderm. If these same algæ are taken in by the brown Hydra they are digested, but, owing to some specific peculiarity of their proper host, the algæ engulfed by the entoderm cells of the green Hydra find a favorable habitat for growth and multiplication. Under the influence of light, the CO_2 given off by the Hydra is employed by the algæ in the synthesis of their carbohydrates, and the oxygen liberated as a result of photosynthesis may be utilized by the Hydra. The mutual services performed on a large scale by the plant and animal kingdoms are thus reproduced in miniature within the limits of a single small organism. The algæ occur in the egg of the green Hydra, and are thereby passed on in the process of sexual reproduction from one generation to the next.

A similar symbiotic relation between one-celled algæ and a small flatworm, Convoluta, has been studied by Keeble, who finds that in *Convoluta roscoffensis* the animal may be entirely dependent upon its algæ for its supply of food. In its early stages this species may devour minute plant and animal organisms, but when its contained algæ increase in number it ceases to take in solid food. For a long time it may live in filtered sea water upon the photosynthetic products of its plant cells.

Finally, in old age, the animal digests its helpful symbiotic companions, loses its green color, and dies. Without its algæ it is unable to live.

If the Convoluta is kept in the dark its algæ decrease in number and finally most of them are digested. The animal grows smaller and paler, but if it is restored to sunlight the algæ multiply, and when this occurs the animal may regain its normal size. Unlike those of the green Hydra, the symbiotic algæ of Convoluta are not transmitted through the egg, and the young larvæ raised in filtered water so as to escape infection were observed to be generally devoid of green cells. If the colorless larvæ were transferred to ordinary sea water they were found to become infected by green cells within a few days. While the algæ as such could not be cultivated independently of the animal, it was found that they gave rise to numerous, free-swimming flagellate organisms which form the means of infecting the young worms.

In Convoluta we have two kinds of organisms which have become mutually dependent to such a degree that neither can complete its life history without the other. The larval worm that does not become infected dwindles and dies. If it is fortunate enough to ingest some algæ it takes on a new lease of life, and "becomes instead of a microscopic, transparent object, a visible green organism." Keeble showed that the algæ were able to assimilate urea, and that they probably subsist in part upon the nitrogenous waste matter of their hosts. They probably furnish their host with sugar, fat, and nitrogenous matter in a form suitable for assimilation into animal tissue.

It has been found that certain tissues of the bodies of higher invertebrates, especially crustaceans, insects, and arachnids, contain numerous bacteria, and sometimes yeast cells and fungi, which have been considered to stand in a symbiotic relation to the cells of their host. The constant association of these organisms with specific tissues, the absence of any indication of injurious effects that can be ascribed to them, and their regular transmission within egg cells from generation to generation,

lend support to the theory that they play some useful rôle in the life of the organism.

Symbiosis is more common among plants than among animals. One whole group, the lichens, containing many families and numerous genera and species, is composed of organisms consisting of fungi and algæ. In the lichen, the algæ are closely enveloped in the network of threads of the fungus. As the fungi, being devoid of chlorophyll, are unable to build up their substance

FIG. 140—A part of a lichen, *Xanthoria parietina: 1*, germinating spore, *sp*, of fungus, whose branches have become applied to two cells of an alga, *a*, *a: 2*, a mass of fungus threads and algæ, *a*, *a*, from the tissue of the lichen. (After Bonnier.)

through photosynthesis, they resemble the bodies of animals in their relations to the algæ. Each partner to the association derives an advantage from the other. While the algæ are generally capable of leading an independent life, the fungi usually do not thrive unless they become associated with algæ.

What are commonly called fungi represent an extensive and miscellaneous assortment of plants that have, as it were, fallen from grace in the sense that they have lost their chlorophyll, and have usually become dependent upon organic matter of some sort for their nutrition. Most of them are saprophytes, or

organisms subsisting on decayed organic material. A great many fungi have become parasitic on other plants or animals. A group of them known as the Mycorhiza have entered into symbiotic relations with the roots of higher plants. The threads of the fungi often form a network about the roots; some kinds penetrate the tissues of the roots, and also extend through the soil. These fungi aid the roots in withdrawing materials from the soil, and in turn they derive sustenance from the roots. Another case of symbiosis in plants occurs in the association between the nitrogen-fixing bacteria and the roots of leguminous plants described in a previous chapter.

In the kind of association known as parasitism one organism makes its living at the expense of another without conferring any compensating benefit. From the point of view of the host, or the organism preyed upon, the parasite is simply a nuisance. Throughout all organic nature we meet the phenomenon of predatory activity. Animals prey upon plants, and larger animals prey upon smaller and weaker ones. But we do not regard wolves as parasites upon sheep, or the sheep as parasites upon grass. The parasite does not devour its victims forthwith; it is in the interest of the parasite not to destroy its host, but to keep it for a permanent supply of food.

Almost all living creatures are preyed upon by parasites. Our own species, despite our exalted position as lords of creation, is attacked by a great diversity of creatures bent upon gaining their living at our expense. Biting flies, gnats, bugs, fleas, mosquitoes, jiggers, lice, ticks, and mites, puncture our skin and live upon our blood. Numerous species of tapeworms, flukes, and roundworms, amounting to nearly one hundred species, inhabit the alimentary canal. The trichina, blood fluke, and hookworm larvæ play havoc in the blood and tissues. Many parasitic Protozoa infest the mouth, digestive tract, and blood. Several kinds of fungi cause distressing diseases of the skin, and the number of species of parasitic bacteria that invade our bodies and produce disease is impossible to estimate. Nevertheless, we are probably no more severely afflicted than other species of

mammals. In fact, we have the great advantage of being able to avoid or get rid of many parasites which less favored animals must passively endure. The organic world is heavily parasitized. Since most species of animals and plants support several kinds of pensioners, the number of species that gain their living at the expense of other organisms is very great. The parasites themselves are by no means free from invasion, and there are sometimes parasites of parasites of parasites.

We have perhaps said enough in a previous chapter about the parasitic bacteria, but it may be remarked here that according to D'Herelle many bacteria are attacked by more minute organisms. To describe in any adequate way the rusts, smuts, mildews, and other fungi that cause plant diseases would require several volumes. There are occasionally parasites among the flowering plants. The mistletoe lives upon branches of trees and sends its rootlets into the bark, where they absorb some of the sap of the host plant. The dodder presents a familar example of a much more degenerate plant that has almost entirely lost its chlorophyll as a result of its parasitic life on other plants. A member of the morning-glory family (Convolvulaceæ), the dodder twines about its host plant, into which it sends absorptive organs of attachment

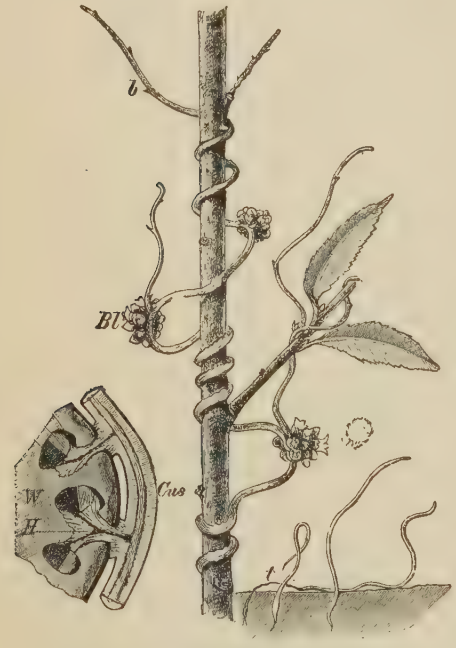

FIG. 141—The dodder twining about the stem of a plant: *b*, rudimentary leaves; *Bl*, clusters of flowers; *t*, young seedlings. At the left is a magnified cross section of the host plant showing the attachment of the dodder, *Cus*, by means of haustoria, *H*, which penetrate the host. (After Strasburger.)

which penetrate to the woody tissues and absorb nutriment from the vascular bundles. The leaves of the dodder are reduced to mere scales, and in the mature plant there is no root. The seeds of the dodder, however, germinate in the soil and produce threadlike seedlings which have the property of swaying about as if in search of some object around which to coil. Should the seedlings fail to effect contact with a suitable plant, they soon die. If the young dodder plant is successful the stem continues to grow, loses its connection with the soil, and comes to depend for nutriment entirely upon its host.

We have already described a few species of parasitic Protozoa, and called attention to a very large group, the Sporozoa, which is exclusively parasitic on other animals. The sponges and the Cœlenterates, with rare exceptions, manage to make their own living, but when we come to the flatworms and roundworms we find whole classes that consist entirely of parasites. One class of flatworms, the Trematodes, or flukes, live upon or within the bodies of other animals. The well known liver fluke (*Fasciola hepatica*), which is often found in the liver of sheep (more rarely in man), well illustrates the complexity of the life cycle through which so many parasitic worms have to pass. This liver fluke is a flattened worm about an inch in length, provided with two suckers, one on the ventral surface and one at the anterior end surrounding the mouth. While in the liver the flukes produce multitudes of eggs which, if they happen to fall into water after they pass out of the body of the host, develop into free-swimming, ciliated larvæ. Should the larvæ encounter the proper kind of aquatic snail, they proceed to bore into its body. Within the snail each larva transforms itself into a sort

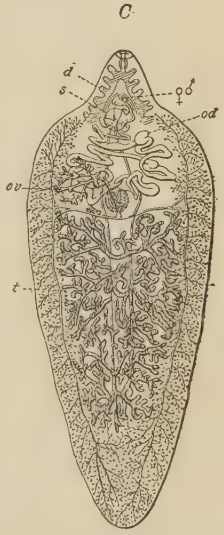

Fig. 142 — Adult liver fluke, *Fasciola hepatica*: *d*, branched intestine; *od*, oviduct; *ov*, ovary; *s*, sucker; *t*, testis. (After Sommer.)

of sac, the sporocyst, inside which are developed other larval forms known as rediæ. The redia is cylindrical in form, furnished with a mouth, pharynx, and short intestine which ends blindly. In the body of the redia other rediæ are produced by a process formerly described as internal budding, but which is now known to be parthenogenesis. After a variable number of generations of rediæ, a somewhat different larval form emerges which is

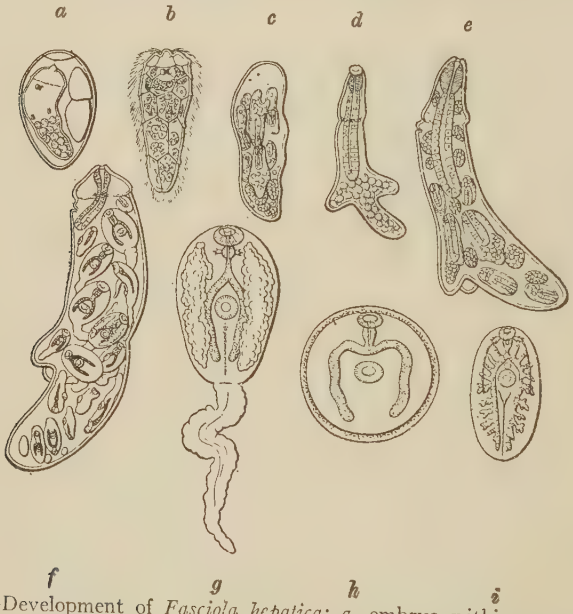

FIG. 143—Development of *Fasciola hepatica: a*, embryo within egg; *b*, ciliated free-swimming larva; *c*, sporocyst developed from the ciliated larva and containing rediæ; *d*, a redia; *e*, an older redia containing other rediæ; *f*, redia containing cercariæ; *g*, a cercaria; *h*, a cercaria encysted; *i*, a young Fasciola. (After Leuckart.)

known as the cercaria. The cercaria is flattened in form, and is furnished with a mouth, two suckers, and a long motile tail. At this stage the larva leaves the body of the snail, swims through the water, and finally attaches itself to grass or other vegetation upon which it encysts. It is in the form of cysts that the parasites are taken into sheep or cattle that feed upon the vegetation near bodies of water. Once in the intestine of their host the cercariæ transform into adult liver flukes.

This roundabout life history, with the numerous chances for failure that it offers for both the original ciliated larva and the cercaria in making connections with the proper animal, is nevertheless an effective means of disseminating the parasite. If there are many larvæ that fall by the wayside, there are great multitudes of them produced. The original Fasciola lays thousands of eggs, and each egg, as a result of the peculiar multiplication that occurs in the larval stages of development, may give rise to over a thousand cercariæ. Each egg may not have more than one chance in a million of forming a liver fluke that gets safely lodged in the bile duct of a sheep. But the species can afford the sacrifice.

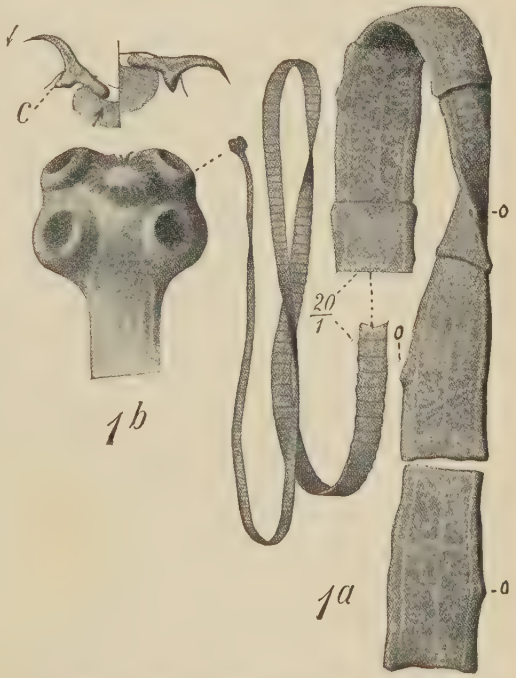

Fig. 144—A human tapeworm, *Tænia solium: 1a*, mature worm; *1b*, scolex with suckers and hooklets, the latter enlarged at *C; o*, opening of sex ducts. (From a Pfurtscheller chart. Courtesy Blakiston's Son & Co.)

In another group of parasitic flatworms, the Cestodes, or tapeworms, adaptation to parasitic life in the intestine of the host animal has led to a complete disappearance of the parasite's own digestive tract. The tapeworm lives surrounded by food that is already digested, and it simply absorbs nutriment through its body wall. At one end the worm is often furnished with suckers or a circle of hooks (sometimes both) for attachment to the intestine of its host. Passing backward from the attached end, the

segments of typical Cestodes become successively larger in size, and the terminal ones are finally constricted off and pass out of the body. At this time they are full of ripe eggs which are set free. If the eggs are taken into the body of a suitable animal they give rise to a larval form which, instead of developing directly into another tapeworm, proceeds to bore through the intestinal wall. It may then be carried by the blood stream to various parts of the body, and after working its way into the tissues it develops into a so-called bladder worm. In the common beef or pork Cestodes, the bladder worm may remain alive for years. Its further development is possible only if it reaches the intestine of another animal, and this only occurs if the second animal devours the flesh of the host. Man becomes infected with tapeworms only by eating raw or insufficiently cooked meat.

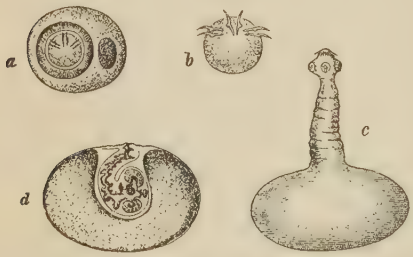

FIG. 145—Development of the bladder worm of the tapeworm *Tænia solium: a*, embryo within the egg; *b*, free embryo with hooklets; *c*, bladder worm with scolex everted; *d*, bladder worm with invaginated scolex. (After Leuckart.)

Either the tapeworm stage or the bladder-worm stage may occur in man, and both stages may be productive of considerable injury. The bladder worms may lodge and grow in delicate organs of the body such as the brain or eye. Leuckart records the case of a bladder worm in a woman's eye where its growth was observed during several years. In *Cœnurus cerebralis*, the bladder-worm stage of which occurs in the sheep, the cyst may reach the size of a hen's egg, and it is therefore a not infrequent cause of death to the animal infected. Usually the bladder worms are much smaller than the adult form, but in Echinococcus they become very large while the mature worm is a diminutive Cestode of only three or four segments. This stage is usually found in the intestine of the dog. The bladder worm is often found in sheep, although it occurs in other animals, and occasionally in

man. It develops into a large, rounded cyst which may attain the size of a man's head and a weight of several pounds. Within this cyst many smaller cysts may arise by a process of budding from its inner wall so that a single egg may eventually produce many worms. Infection by the bladder-worm stage is acquired by swallowing the eggs of the mature worm, and the latter is acquired by eating flesh containing the cysts. Carnivores and herbivores constitute the two hosts which are normally required for the completion of this highly modified life history.

Another common group that furnishes numerous parasites is the Nematoda, or roundworms. The large *Ascaris lumbricoides*, which may attain the length of eight inches, is an occasional inhabitant of the human alimentary canal that sometimes causes serious trouble, especially in children. A more dangerous parasite is the very much smaller trichina (*Trichinella spiralis*). Like the common human tapeworms, this species has a free stage in the intestine, and an encysted stage in the tissues, and it likewise requires two hosts, the eater and the eaten, for the completion of its life cycle. Should we be indiscreet enough to eat raw or insufficiently cooked pork, we might take into our digestive tract a number of encysted trichinæ. Under the beneficent influence of our digestive juices the little encysted worms which have been living in an immature and dormant state in the tissues of the pig now respond to the opportunity for which they have long been lying in wait; they emerge, grow, become sexually mature, mate, and produce their broods of young. The latter proceed to bore into the walls of the intestines. Many of them are carried by the blood to different parts of the body, where they penetrate the tissues and become encysted. When the little parasites are actively invading the body the infected individual is apt to be having a bad time. Many persons have died as a result of a heavy infection of trichina. Inspection of meat and precautions to prevent swine from eating the flesh of animals

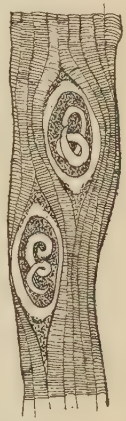

FIG. 146—Two Trichinæ encysted in muscle. (After Leuckart.)

such as rats which carry the encysted worms, have materially reduced the damage done by this parasite.

Another one of our small nematode enemies is the hookworm, which is unfortunately very prevalent in many of the warmer parts of the world. Persons infected by this parasite frequently become anemic, lose vitality and energy, and are unusually prone to succumb to other diseases. The parasites in the adult stage usually occur in the intestine, but the larvæ are often found in the blood and tissues. The young worms that reach the lungs work their way out of the blood vessels into the air passages, creep up the windpipe to the throat, and are then carried down the esophagus to the stomach whence they readily pass into the intestine. The complete life history of the hookworm was for a long time unknown. Infection was found to be common in people working in mines, and among those whose life brought them into frequent contact with damp soil. Such people were known to be troubled occasionally with what was called ground itch, but no connection between this malady and hookworm was suspected. The eggs of the hookworm pass out in large numbers from the human intestine and hatch in damp soil or water into active larvæ. While studying these larvæ Looss happened to place some water containing them upon his hand, and he soon felt a pricking sensation which led him to discover that the young larvæ were boring into his skin. He also placed a culture of larvæ on a child's leg which had to be amputated, and he was able to follow the different stages by which the larvæ penetrated the skin and gained access to the blood vessels.

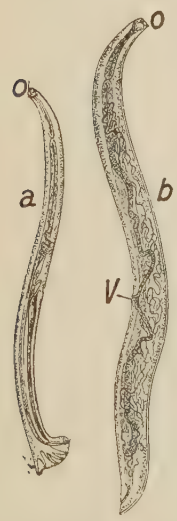

FIG. 147—The hookworm: *a*, male; *b*, female; *o*, mouth; *V*, opening for discharge of eggs. (After Leuckart.)

Although hookworms may be taken directly into the alimentary canal by means of food or drinking water, the feet afford the most frequent portal of entry into the body. Adequate care in the disposal of human excrement, so as to prevent the contamination

of the soil by the eggs has done much to check the spread of this troublesome pest. Fortunately hookworm infection yields quite readily to proper medical treatment. The hookworm campaign carried on by the United States Government and the Rockefeller Institute in the southern states has produced splendid results. Thousands of children and adults have been rescued from the ravages of these intestinal parasites from which they have suffered so long in ignorance of the cause of their affliction.

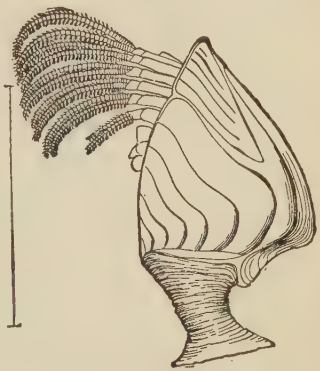

FIG. 148—A goose barnacle, *Lepas fascicularis*. (After Smith.)

Parasitic crustaceans are many, and belong to several groups. One order, the Copepoda, includes a great many parasitic species which occur with especial frequency upon fishes. Another order, the Isopoda, also furnishes many species of fish parasites, and the related order of Amphipoda includes the parasitic family of Cyamidæ, or whale lice. Among the barnacles there are several species which are parasitic chiefly upon other kinds of crustaceans. Nearly all the parasitic crustaceans exhibit, to a greater or less degree, the degeneration

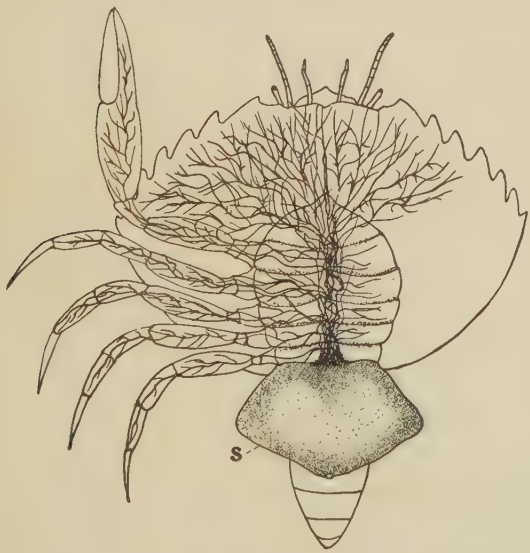

FIG. 149—The adult Sacculina attached beneath the abdomen of a crab and penetrating with its rootlets the body of its host.

which so frequently results from a parasitic mode of life. One of the most extreme cases of degeneracy is afforded by the parasitic barnacle Sacculina which lives attached to the abdomen of crabs. This parasite, which has the appearance of a swollen sac, absorbs its nutriment by means of rootlets which ramify within the tissues of its host. The eyes, mouth parts, thoracic appendages, segmental structure, and many complex organ systems characteristic of a typical barnacle have completely disappeared, and were one unfamiliar with the embryonic and larval history of Sacculina there would be almost nothing to indicate its affinities with the Crustacea. The fact that the eggs of Sacculina hatch into free-swimming nauplius larvæ of the type characteristic of barnacles, and that several successive stages of its development are closely similar to those which are passed through by other barnacles, gives us an unmistakable clue to the relationships of this aberrant form. If the larva in the course of its swimming encounters a proper sort of crab, it attaches itself, sends rootlets into its host, and undergoes a profound degeneration of structure in which all semblance to its early crustacean stages of development disappears.

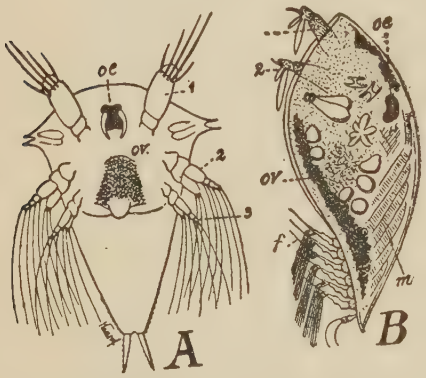

FIG. 150—Nauplius, *A*, and Cypris stage, *B*, in the development of Sacculina: *f*, thoracic appendages; *m*, muscles; *oc*, nauplius eye; *ov*, ovary; *1*, *2*, *3*, first, second, and third appendages corresponding to the first and second antennæ and mandibles of adult crustaceans. (After Delage.)

The group of arachnids contains numerous parasites many of which have become much reduced in size and degenerate in structure. The ticks are bloodsucking parasites, chiefly of mammals and birds. One species of tick is responsible for the transfer of the minute sporozoön which causes Texas fever in cattle. Another species transfers the germ of the Rocky Moun-

tain spotted fever in man. The numerous mites which infect plants and animals are mostly diminutive, and some of them, such as the species which causes the itch in human beings, are almost invisible to the naked eye.

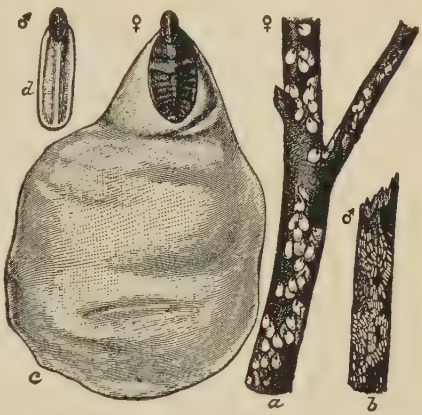

FIG. 151—The scurfy bark-louse: *a*, female scale bugs; *b*, male scales; *c*, female scale enlarged; *d*, male scale enlarged. (After Howard.)

Among the insects, parasitism assumes a number of very diverse forms. Perhaps the extreme of degeneracy is found in the wingless and almost immobile scale bugs. Parasitism has not infrequently led to degeneracy among insects, but there are numerous species in which it does not have this effect. In many cases this is probably due to the fact that parasitism is confined to the larval stage of development. The flies of the family Tachinidæ lay their eggs upon the bodies of other insects, and especially upon larvæ. The young larval parasites that hatch from the eggs bore into the body of their host and live upon its tissues. Somewhat similar habits are found in the ichneumon flies and their relatives among the Hymenoptera. The larvæ of many of the smaller species live within the eggs of other insects. The ichneumon *Pimpla conquisitor* pierces the cocoon of the tent caterpillar and deposits her eggs upon the pupa, and the larvæ, when they hatch out, proceed to devour the helpless pupa at their leisure. Another ichneumon, *Thalessa lunator,* has a remarkably long ovipositor with which she bores into wood until she reaches the burrow of the

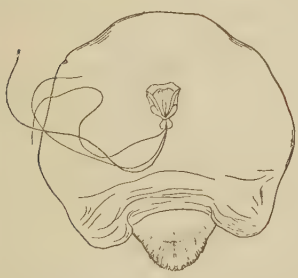

FIG. 152—Ventral view of female red scale detached and showing the long sucking stylets.

larva of a wood-boring sawfly, Tremex. When the egg hatches the young larva crawls along the burrow until it reaches its victim, which it proceeds to devour. The solitary wasps may be regarded as parasitic in their larval state, since the mother wasp usually lays her egg upon her prey without killing it, thus allowing her larva to feed upon the tissues of a living organism.

FIG. 153—The ichneumon fly, *Thalessa lunator*, in the act of boring into wood with her ovipositor. (After Reilly.)

The insects whose larvæ lead a parasitic life are mostly very active, alert, and discriminating creatures which exhibit complex and highly specialized behavior in providing for the welfare of their progeny. Parasitism of this particular kind would seem, therefore, to favor the development of more highly organized forms. Degeneracy would be quite inconsistent with the exacting requirements which it imposes.

FIG. 154—*Lysiphlebus*, in the act of depositing an egg within the body of an aphis. (After Webster.)

We have described only a few of the more common kinds of associations between organisms, but there are many other kinds of which we must omit any mention. The plants and animals of any limited area have numerous interrelations and may be said to constitute a sort of society. Insects and flowers are united in a relation of mutual service. Herbivores devour plants, and carnivores prey upon herbivores. Birds eat the seeds of plants and destroy insects that are injurious to plant life. Parasites

attack all kinds of organisms, and bacteria and fungi resolve the dead bodies of plants and animals into simpler constituents that constitute the food of plants. A great increase of insect life favors the multitudes of spiders, and insectivorous birds and mammals, and thus the undue preponderance of insects is checked. The organic life of a given locality subsists in a sort of balance which tends to be maintained because disturbances of the balance tend sooner or later to bring about their own remedy. This may be well illustrated by a passage from Darwin. After speaking of the influence of cattle in checking the growth of Scotch fir, he remarks:

> In several parts of the world insects determine the existence of cattle. Perhaps Paraguay offers the most curious instance of this; for here neither cattle nor horses nor dogs have ever run wild, though they swarm southward and northward in a feral state; and Azara and Rengger have shown that this is caused by the greater number in Paraguay of a certain fly, which lays its eggs in the navels of these animals when first born. The increase of these flies, numerous as they are, must be habitually checked by some means, probably by other parasitic insects. Hence, if certain insectivorous birds were to decrease in Paraguay, the parasitic insects would probably increase; and this would lessen the number of the navel-frequenting flies—then cattle and horses would become feral, and this would certainly alter (as indeed I have observed in parts of South America) the vegetation: this again would largely affect the insects; and this, as we have just seen in Staffordshire, the insectivorous birds, and so onwards in ever-increasing circles of complexity. Not that under nature the relations will ever be as simple as this. Battle within battle must be continually recurring with varying success; and yet in the long-run the forces are so nicely balanced, that the face of nature remains for long periods of time uniform, though assuredly the merest trifle would give the victory to one organic being over another.

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CHAPTER XIII

REGENERATION, EXPERIMENTAL EMBRYOLOGY, AND THE REGULATION OF ORGANIC FORM

The activities described in previous chapters are mainly those which form a part of the usual routine of living. But the course of life is not always suffered to run on smoothly. Living beings are subjected to mutilations, distortions, and many other abnormal modifications, and the ways in which they meet these various mishaps afford some of the most striking manifestations of the phenomena of life.

Everyone is familiar with the fact that many organisms are able to regenerate lost parts. A lizard may form a new tail, and a newt may regenerate a lost leg or eye. The power of regeneration is generally greater in the lower and simpler forms of life. The trumpet-shaped infusorian Stentor may be cut into several pieces, and each piece, provided it contains a part of the long, moniliform nucleus, will transform itself into a new Stentor similar to the original one except in size. Lillie has shown that a fragment as small as one sixty-fourth of the original Stentor may form a new individual.

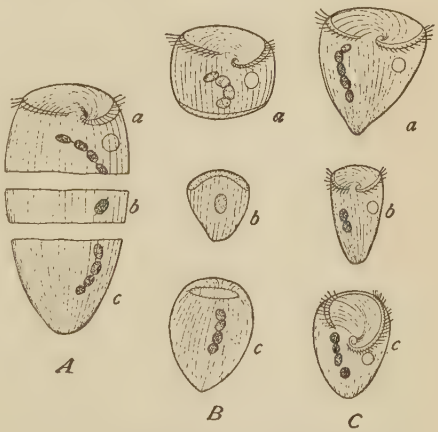

FIG. 155—Regeneration of the infusorian, Stentor: *A*, Stentor cut into three pieces; *B*, *C*, successive stages in the regeneration of the pieces, *a*, *b*, *c*. (From Gruber, after Balbiani.)

The fresh-water Hydra has long been a favorite subject for the study of regeneration ever since the Abbé Trembley per-

formed his well known experiments on this animal in 1739. One may cut the Hydra into several pieces and each will transform itself into a smaller individual. Tentacles grow out at the end of the piece that was near the oral, or mouth end of the body, while the opposite extremity forms the foot. In some instances, new Hydras have been regenerated even from the isolated tentacles. If the body is cut in two longitudinally the edges of the half-cylindrical pieces close together, new tentacles are budded out at the oral end, and a perfect form is finally attained.

The hydroids, like Hydra, exhibit marked powers of regeneration. The end of pieces nearest the oral end generally regenerates tentacles, while the reverse end produces the rootlike stolons by which the hydroids are usually attached to some solid object. This polarity, as it is called, may sometimes be reversed under the influence of the proper external conditions. If a piece of Tubularia is cut from near the middle of the stem, and the end that was nearest the oral extremity of the hydroid is placed in sand, the opposite end of the piece will produce tentacles and a mouth, while the buried end produces a stolon.

In recent years a large amount of experimental work has been done on the common fresh-water planarians, since these forms are even more favorable for such investigations than Hydra or the hydroids. These worms have an elongated, flattened body, and a pointed head bearing a pair of eyes situated near the brain. The mouth is at the end of a muscular pharynx which protrudes from near the center of the body. When a planarian is cut across near the middle, new cells are formed at the cut end of both pieces, and the anterior half regenerates a new tail while the posterior half forms a new head. If a planarian is cut longitudinally down the middle, each half regenerates the missing part. Even relatively small pieces, less than a tenth of the entire animal, will regenerate a whole planarian less than a tenth the usual size. Each of these small planaria may be cut into several pieces which regenerate into smaller individuals, and the latter may be again subdivided into still smaller ones. By this method it is possible to obtain planarians of less than one-thousandth

the size of the original animal, but a limit is soon reached beyond which further regeneration no longer occurs. An investigation of the cells of these diminutive individuals showed that they are not reduced in size; they are simply fewer in number. Not improbably this fact imposes a limit to the reduction in size due to successive regenerations. There has to be a certain number of cells in order to form the various organs of the planarian's body, and if the number were too much reduced there would not be enough of them to go around.

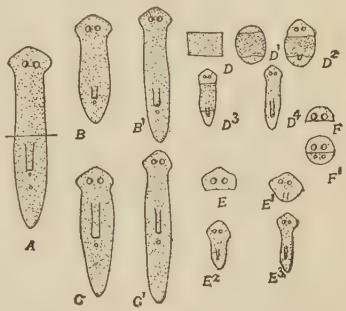

FIG. 156—Regeneration of *Planaria maculata: A*, Planaria cut across the middle; *B*, B^1, regeneration of anterior half of *A; C*, C^1, regeneration of posterior half of *A;* D^1, D^2, D^3, D^4, stages in the regeneration of a short piece, *D; E*, E^1, E^2, E^3, regeneration of a Planarian from a head, *E;* F^1, heteromorphic regeneration of a head on the posterior end of an old head, *F*. (After Morgan.)

It has been found that if very short pieces are taken from a planarian they may, at times, regenerate a head at the posterior, as well as the anterior end. The development of a part different from the one removed is called heteromorphosis. This phenomenon may be observed also in pieces cut from near the posterior end of an earthworm, which regenerate a tail at their anterior cut surface instead of a head. A striking instance of heteromorphosis has been observed in several species of crustaceans which regenerate an antenna-like organ instead of an eye. In order to produce this result the eyestalk must be cut off far enough down to remove the optic ganglion.

The regeneration of a protozoön, a hydroid, and to a certain extent a planarian, involves the transformation of the old part into a complete new organism—a process known as morphallaxis. In higher animals new cells are produced at the cut surface and these are fashioned into the form of the missing part. This is what occurs when a crab renews its missing claw or a newt grows a new leg. The appendages of many crustaceans and of some insects are provided with a so-called breaking joint near the base

where they are especially liable to be broken off, and from which they regenerate more readily than from other levels. After the loss of some of the terminal segments, the part of the leg beyond the breaking joint may be cast off and the leg regenerated from this point. When a crustacean is seized by one of its appendages the creature may leave this part of its anatomy in the possession of the enemy and regenerate a new appendage at its leisure. For the crustacean this self-amputation is an adaptive device, since it is obviously better to lose a part than the whole. Similar tricks are commonly performed by the brittle-stars and occasionally by starfishes, both of which have the power of regenerating their missing arms, or rays. In some species of starfish a single ray may regenerate the entire animal.

Among the vertebrates the power of regeneration is well developed only in the lower classes. Fishes may regenerate parts of their tails and fins, and the newts may restore a missing tail, leg, or even eye. Lizards may renew a missing tail, but not a lost leg. Birds have been known to regenerate a considerable part of the bill, and they regularly renew their feathers, but otherwise their capacity for the regeneration of lost parts is very limited. This capacity is even less developed among the mammals.

In the higher animals greater power of regeneration is often manifested in internal organs and tissues than in external parts. When a nerve is severed the part of the fiber cut off from its connection with the nerve center degenerates, but new fibers grow out along the path of the degenerated nerve and make connection with the terminal organ. Broken bones form new cartilaginous tissue at the point of fracture, and this tissue finally ossifies so that the two parts become firmly knit together. Denuded epithelium is rapidly restored, and the connective tissue elements as well as the epithelium of the skin are often replaced by a new growth. A certain degree of regenerative capacity is exhibited in the healing of wounds, and the replacement of the outer dead cells of the skin by new cells formed in the deeper layers of epithelium. It is exhibited also in the production

of new blood corpuscles, in the renewal of hair, and in many other ways throughout the body. Regenerative processes graduate insensibly into the ordinary physiological activities of the body so that they cannot be separated except in an arbitrary manner. In fact, all life involves a continual process of regeneration.

The power of regeneration is generally greater in young

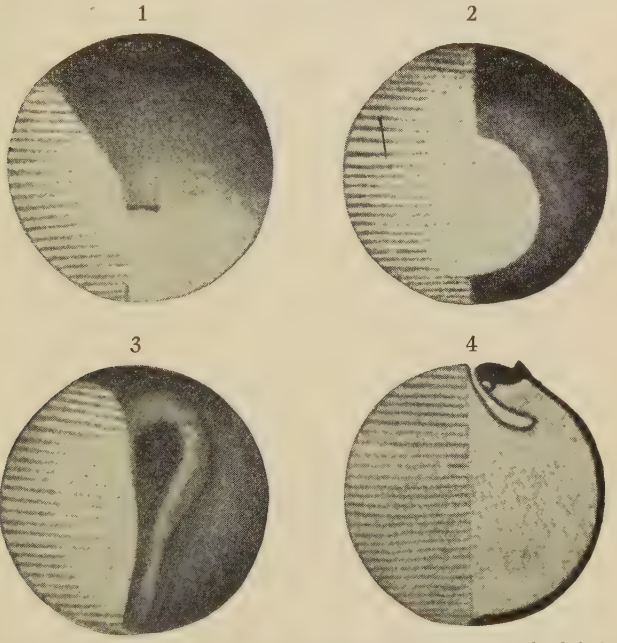

FIG. 157—Partial development of the frog's egg after injury to the left half: *1*, *2*, beginning and later gastrula; *3*, right half of medullary folds and groove; *4*, cross section through stage shown in *3*. (After Morgan.)

animals than in older ones. In conformity with this fact, the regenerative capacity of the embryo is usually greater than that of the developed body. If the eggs of a sea urchin are separated in the two-, four-, or eight-cell stage, each cell may develop into an embryo of one-half, one-quarter, or one-eighth of the usual size. In some medusæ each cell of the sixteen-cell stage may divide much like the original ovum and develop into a perfect embryo. If the cells of the egg of a sea urchin are separated in the two-cell stage each cell divides at first as if it constituted a

part of a normal embryo, and forms a half-blastula which later closes in to form an entire gastrula. On the other hand, when the eggs of the mollusc Dentalium are divided in the two- or four-cell stage, each fragment produces a half or a fourth larva instead of a complete larva of smaller size. Similar phenomena of partial development, as it is called, occur in the eggs of cteno-

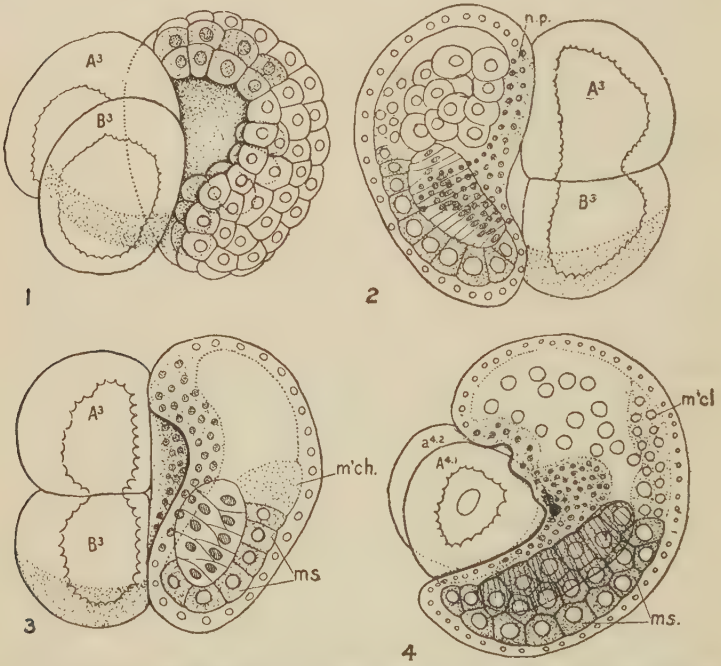

FIG. 158—Partial development of the egg of the tunicate *Cynthia* (*Stycla*) *partita*, after one or two cells have been killed in the four-celled stage: *1*, right half gastrula; *2*, left half gastrula showing notochord and muscle cells; *3*, right half embryo; *4*, right three-fourths embryo; *m'cl*, *m'ch*, mesenchyme; *ms*, muscle cells; *n. p.*, neural plate; A^3, B^3, $A^{4\cdot2}$, $A^{4\cdot1}$, killed cells. (After Conklin.)

phores, tunicates, and some species of worms. If one of the cells of the frog's egg is killed in the two-cell stage (it is difficult to separate the cells on account of their large amount of yolk), the remaining cell forms a half-embryo. Later this part may regenerate the missing half. It is possible, however, to obtain two embryos from a single frog's egg if the egg is held in an inverted

position after the first division is completed; there appears to be a rearrangement of the contents of the egg so that each cell develops independently into a perfect embryo.

The isolated cells of the eggs of different animals thus react in quite different ways. In some cases, each cell behaves much like the entire egg in exhibiting a capacity to produce the entire organism; in others, the cells appear to become specialized very early so that, if separated, they undergo a strictly partial development. Perhaps these differences are due to the different periods at which the egg protoplasm becomes differentiated. Where it remains plastic each isolated cell may produce a small embryo; where it acquires a certain set at an early period development may be of the partial type. One may observe in some forms a differentiation that appears during the very first division of the egg. Conklin has described the sorting, or parceling, out of certain visibly different materials in the first cleavages of the egg of the tunicate Cynthia, and it is probable that this differentiation is closely associated with the partial development that occurs in this form.

The capacity of an isolated cleavage cell to produce an entire embryo is very intimately related to the phenomenon of regeneration. In both cases the part restores the whole. It may not be inappropriate to speak of development as the regeneration of an individual from a single cell. The relation between regeneration and reproduction by budding or fission is sufficiently obvious. A planarian normally divides by transverse fission, and each part forms anew whatever is lacking to produce a complete organism. If we cut the creature across with a knife we are not doing anything very much different from what the animal does of its own accord, and the processes by which each part becomes a whole are much the same in either case.

Organisms attain to normal wholeness by other processes besides regeneration. Professor H. V. Wilson has cut up sponges and rubbed them through fine bolting cloth so as to separate them into their component cells. Masses of these cells placed in sea water were found to coalesce and finally develop into a

sponge. Cells from different individuals could be made to unite in this way to form a new organism. Similar experiments were found to be successful with several species of hydroids. Garbowski separated the cells of a number of blastulæ of the sea urchin and pressed together the cells belonging to different animals. These secondary aggregations were found to develop into perfectly normal larvæ. The phrase "cell state" which has often been applied to the multicellular organism would seem to possess a peculiar appropriateness when applied to these composite individuals.

The maintenance of the normal form of a body involves the regulation of the proportionate sizes of its various parts. When an infusorian divides, each half is transformed into an organism of one-half the usual size. This means that certain parts are reduced while other parts are formed anew. The piece is, as it were, made over so that all organs stand in much the same size relations to each other as they occur in the original organism. Whether regeneration is effected by the formation of new tissue and its subsequent transformation into the missing part, or by working over the part into a smaller whole, there goes on a process of mutual adjustment between the different regions of the regenerating organism. Doubtless these balancing-up processes occur in the organism at all times in order to keep the different organs in their proper relations to each other, and to secure the coördinated functioning of the whole body. Development by which the form of the organism is attained, regeneration by which the normal form is restored after loss, and the many adjustments of growth processes and functional activities always going on within the organism by which the normal form is retained, all appear to be guided so as to achieve a certain end—the preservation of the integrity of the organic whole.

Efforts to explain this striking feature of organic life have given rise to a number of theories of development and regeneration. We have briefly alluded in the ninth chapter to the theory of preformation by which some of the earlier embryologists endeavored to interpret the development of the body. In its extreme form, the doctrine of preformation was not so much an

explanation of development as a denial that development really takes place. The old theory is now dead, but it has left a number of descendants. Of the modern forms of the doctrine, what is called the Roux-Weismann theory has perhaps attracted the greatest amount of attention. This theory postulates that in the nucleus there are numerous different kinds of germinal units which guide the development of particular parts of the body. These units are arranged in a definite manner in the chromosomes of the nucleus and during the successive cleavages of the egg, the units come to be parceled out so that they lie in different regions of the embryo, each region differentiating in a particular way determined by its own peculiar variety of germinal unit. Weismann, who has elaborated this theory in the greatest detail, holds that the germ plasm has a complex architecture, and that during each cleavage the nucleus divides into two qualitatively different parts. Development therefore depends upon a kind of sorting process by which the organized germ plasm is unpacked and distributed in a very orderly and definite manner. As cleavage goes on, the nuclear material becomes more and more simplified. The theoretical limit of this procedure is reached when a nucleus contains only one kind of germinal unit, or determinant. This kind of unit would then determine the part to develop into muscle fibers, nerve cells, or a bit of epithelium, according to the nature of the unit that fell to its lot.

Weismann has applied his theory to the explanation of regeneration as well as development. It is assumed that parts commonly contain other determinants besides those which control the differentiation of a given organ. These may be regarded as reserve, or supplementary determinants whose potencies may be set into activity by the altered conditions resulting from the loss of a part of the body. When a crab grows a new claw, the determinants for the claw in the remaining stub of the leg are supposed to multiply and effect the restoration of the missing appendage. Where organs cannot be regenerated this is due, according to Weismann, to the fact that the necessary determinants are not present in the adjacent parts.

The Roux-Weismann theory encounters certain difficulties in the experiments which have been described on the isolation of cleavage cells. If a single cell of the eight-cell stage of a jelly-fish egg can produce a perfect embryo, one must postulate that, notwithstanding the qualitative divisions of nuclear material that are supposed to occur, a certain amount of unmodified germ plasm is passed on to all the early cleavage cells. This supposition leads to a complication of the original hypothesis, and when we apply it to such cases as the regeneration of an entire Begonia plant from a fragment of a single leaf, the amount of reserve germ plasm which is carried on to late stages of development is so great as to render practically useless the original assumption of the theory.

The doctrine also encounters difficulties on account of the fact that eggs may be distorted through pressure so as to force the nuclei to occupy positions different from those which would be taken in normal development. Since normal embryos result after the release of pressure, it indicates that the direction in which a part of the embryo differentiates is independent of the particular derivation of its nuclei. All the facts of observation and experiment tend to show that the nuclei in early development are qualitatively alike. This is indicated by the experiment of forming a normal embryo from massing together the separated cells of a number of different eggs, and the fact that two embryos have sometimes been fused together to form a single normal individual. In these cases it cannot be the particular source of the nuclei, or even the cytoplasm, that determines how a part develops. It is rather the relation in which the part stands to the whole. These experiments bear witness to the truth of the aphorism of Driesch that "the fate of a cell is a function of its position." In some forms the cleavage cells become specialized early so that they cannot be diverted from developing in their own way after they are separated, but this fact does not alter the fundamental truth embodied in Driesch's statement.

According to the theory of germinal localization advocated by His (another form of the doctrine of preformation), the individual

egg is marked off into regions which stand in a fairly definite relation to the organs to which they give rise. These regions are supposed to contain peculiar organ-forming substances which determine how the parts will develop. The theory postulates a cytoplasmic, instead of a nuclear preformation, and although there is a certain amount of cytoplasmic organization in the undivided egg, the theory breaks down when we attempt to apply it as a general explanation of development. In fact, any kind of preformation theory of development meets with serious difficulties in the experiments just mentioned. The experiments clearly indicate that the way in which a part develops is largely a result of the interaction of its components. The whole seems, in some way, to dominate the part and make it conform. How is this control exercised?

The theories which interpret form production in organisms as a phenomenon akin to crystallization appear to explain this control rather better than the theories of the Roux-Weismann type. We may select, as a representative of this second class of speculations, the theory set forth with characteristic ingenuity by Herbert Spencer. According to Spencer's theory, living matter is composed of units called physiological, or later constitutional, units which are supposed to possess the attribute of polarity in obedience to which they arrange themselves into a definite form. In the first chapter we alluded to the power of regeneration possessed by crystals, a power dependent upon the kind of polarity in the molecules of which the crystal is built. According to Spencer the physiological units exhibit a similar property, in that they "have an innate tendency to arrange themselves into the shape of the organism to which they belong." The analogy between regeneration in crystals and regeneration in living beings is indeed striking, but is it anything more than analogy?

An organism differs markedly from a crystal, which is a static thing, in being in a state of continual flux. It is a moving instead of a stationary equilibrium. It contains many diverse parts instead of being composed of the same kind of structural elements

throughout. And the methods by which its missing parts are restored differ profoundly from the regenerative processes of the crystal. That the regenerative processes in organisms and crystals are closely related phenomena cannot, therefore, be considered as proven, or perhaps even as probable, at the present time.

For the vitalist, regeneration is a phenomenon that is inexplicable in terms of physical and chemical laws. Driesch, for instance, would interpret form production of all kinds as the result of an entelechy, or vital principle, which shapes the constructive processes in an organism so that they realize a certain end result. One of the striking peculiarities of formative processes is that they may produce a given organ by a variety of methods. While there are generally certain similarities between the way in which organs are regenerated and the way in which they were originally formed in the embryo, there are many cases in which these processes differ profoundly. Organs formed from one germ layer are sometimes regenerated from a different germ layer. The regeneration of the lens of the eye of a Triton, for instance, has been found to take place by a method that is very different from its original production. In the embryo, the lens of the eye arises as a thickening of the ectoderm where the optic cup, which grows out from the brain, comes in contact with the outer covering of the head. This thickening sinks in, becomes detached from the surface layer, and transforms into the lens. If the lens of the adult Triton is removed, the cells of the upper margin of the iris proceed to multiply and form a mass out of which a new lens is gradually differentiated. The epithelium of the iris and the embryonic epithelium from which the lens originally developed are both ectodermic; nevertheless, they have had a very different embryonic history from an early period of development. Here is an impressive illustration of the resourcefulness of the organism in replacing a missing structure. It is not surprising that the vitalists frequently cite it with an air of triumph in supporting their position.

Much experimental investigation has been devoted, during

the last thirty years, to the attempt to ascertain the causes of developmental and restorative processes. Not content with describing what takes place, the modern biologist is endeavoring to ascertain why the phenomena take place as they do. This leads to experimentation with the aim of analyzing the phenomena into their component factors. Much has been learned in this way in regard to the mutual dependence of parts during development and regeneration. Perhaps with increasing knowledge and insight, the orderly building of the organic body may some day be explained, but at present this is only a pious hope.

Undoubtedly biologists are a long way from giving a physical or chemical explanation of the production of organic form. A closer approach toward an understanding of this enigma is made, we believe, by those theories which view form production as the result of physiological interadjustments. The doctrine of metabolic gradients put forward by Dr. C. M. Child has brought out an important relation between intensity of metabolism and differentiation in regenerating and developing organisms. The part of a planarian, for instance, in which the rate of metabolism is the highest, tends to differentiate into a head, and this, according to the theory, dominates the differentiation of the parts lying behind it. It is doubtless true that metabolic gradients are intimately associated with the localization of differentiating activities. They perhaps afford what Herbst has called formative stimuli in development and regeneration.

According to a physiological theory of form regulation propounded a few years ago by the present writer the production, regeneration, and maintenance of the normal form of the organism are the outcome of an essentially symbiotic relation subsisting between its various parts. Each part of the organism is assumed to derive certain advantages from the substances or stimuli received from neighboring parts, and these, in turn, receive corresponding advantages from it. If a small part of an organism is removed, and cells of a relatively unspecialized character are produced in its stead, as in fact they commonly are,

in what direction would these cells tend to differentiate? As a result of the environment of these cells a sort of premium would be placed upon development in the direction of the missing part, since this would secure whatever advantages were afforded by the symbiotic relation. Regeneration in an organism would therefore have a certain analogy with regeneration in social groups. If all bricklayers should suddenly disappear, their ranks would soon be filled by other people who would respond to the increased demand that would be created for this particular kind of workers. The similarities in the processes of regeneration and adjustment that go on in the individual and in the social group represent something more than mere analogy. Both societies and individual organisms are composed of units which tend to grow and perpetuate their kind. The units of both have a considerable degree of plasticity, especially in early stages, and what each unit may become is largely determined in accordance with the principle of supply and demand as well in the individual organism as in human industrial society. That "the fate of a cell is a function of its position" is precisely what would be expected in accordance with the theory here set forth.[1] Position means a certain complex of stimuli from adjacent parts which determine the direction in which a part develops.

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[1] The theory which is here very briefly and inadequately expounded is more fully elaborated in an article on "The Problem of Form Regulation," published in *Roux's Archiv f. Entw. Mech.*, 17:265–305 (1904).

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CHAPTER XIV

HEREDITY AND VARIATION

The field of biology which has seen the most rapid advancement during the last quarter century is unquestionably genetics, or the science which is concerned with heredity and variation. Balzac once remarked that heredity is "a maze in which science loses itself." This statement correctly described the situation at the time it was written, but it is true no longer. So rapidly indeed has genetics advanced that it has become the one department of biology which perhaps approaches most nearly the status of an exact science. Professor Bateson has stated that "an exact determination of the laws of heredity will probably work more change in man's outlook on the world and in his power over nature, than any other advance in natural knowledge that can be clearly foreseen." This was written in 1900 just after the rediscovery of Mendel's law of heredity. The remarkable progress in genetics to which I have referred has gone far toward justifying Professor Bateson's prophecy. The man primarily responsible for bringing genetics out of its previous Egyptian darkness was Gregor Johann Mendel, and it is no exaggeration to say that more has been learned about heredity and variation since Mendel's discoveries became generally known than had been learned in all preceding time.

Mendel was an Austrian priest who was engaged as a teacher of natural science for several years at Brünn, Austria. During his leisure time he occupied himself with experiments on hybridizing plants, and he published the results of his researches in two papers that appeared in the *Proceedings of the Natural History Society of Brünn* for 1865 and 1869. Although these papers contained the announcement of the most important generalization ever made in the study of heredity, they remained

practically unnoticed until, through a curious coincidence, they were brought to public attention independently by three men, De Vries, Correns, and Tschermak, in the year 1900. The beginning of the twentieth century thus formed the beginning of a new era in the study of genetics.

Mendel's most significant experiments were performed upon the varieties of the common garden pea, *Pisum sativum*. These varieties are commonly distinguished by the possession of one or more characters which are quite sharply defined. One variety, for instance, is characterized by its dwarf stature; another by possessing wrinkled seeds instead of round ones, and another by having green instead of yellow seed coats. In crosses, Mendel found that these characters were capable of being combined in various relations with other characters. Some characters were found to prevent the appearance of others. Such were designated as dominant, while the suppressed character was called recessive. If, for instance, a tall pea is crossed with a dwarf variety the immediate progeny (commonly called the first filial, or F_1 generation) will all be tall. The character of dwarfness is recessive to the character of tallness, which is dominant. Similarly, in the cross between a pea having round seed and a pea having wrinkled seed the F_1 generation consists entirely of round peas. The recessive characters of dwarf stature and wrinkled seed are not lost, however, as is shown by raising a second generation from the F_1 progeny. If the plants of the F_1 generation of a cross between a tall and a drawf pea are allowed to pollinate themselves, or if two members of this generation are crossed, the recessive character of dwarfness reappears. The remarkable peculiarity of this second, or F_2, generation is that the talls and the dwarfs occur in a definite numerical ratio, there being three

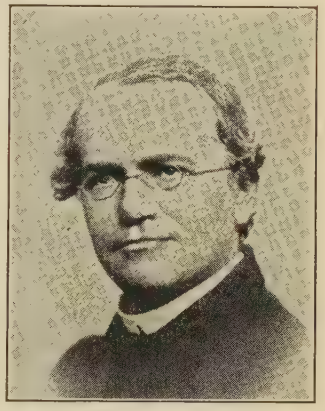

Fig. 159—Gregor Mendel.

times as many tall as dwarf plants. Likewise the F_2 generation of a cross between a round and a wrinkled pea contains three times as many round as wrinkled seeds. These ratios do not, of course, always appear in any particular family of limited numbers; they are the ratios which are observed when sufficiently large numbers of progeny are obtained to eliminate the effect of chance.

FIG. 160—The results of crossing two kinds of nettle, *Urtica*, the leaves of the one, *pilulifera*, with sharply serrate margins, those of the other, *dodartii*, with nearly smooth margins. The serrate margin is dominant and is shown in the first generation, *I. Gen.* In the second generation, *II. Gen.*, there are three serrate- to one smooth-leafed plant. One-third of the dominants produces nothing but serrate-leafed forms in the third generation, *III. Gen.* Two-thirds of them produce three serrate to one smooth form and the smooth-margined forms breed true. (After Correns.)

In the second generation of a cross between peas with yellow seeds and peas with green seeds, Mendel obtained 6022 yellows, and 2001 greens, which is a very close approximation to a 3:1 ratio, green being in this case recessive to yellow.

The dwarf, wrinkled, or green peas reappearing in the F_2 generation were found to breed true if crossed with their own

kind or allowed to pollinate themselves. It is quite otherwise with the peas exhibiting the dominant character. Only some of these breed true; others give rise, like the F_1 generation, to both dominant and recessive individuals in the ratio of 3 to 1. The former are called homozygous and the latter, or mixed forms are called heterozygous. The pure, or homozygous dominants, moreover, were found to occur in a definite numerical ratio to the impure dominants, there being on the average one of the former to two of the latter. Designating the pure dominants by the letters DD, the recessives by RR, and the mixed or heterozygous forms by DR, we may write the general formula for a second, or F_2 generation in a simple Mendelian cross as

$$1\ DD + 2\ DR + 1\ RR.$$

This is the formula for the so-called monohybrid ratio, or the typical ratio observed in the second generation of a cross between forms differing in a single character. The same formula was found to apply to all the seven pairs of characters, which Mendel investigated in the garden pea.

To the biologist the fact that characteristics should present themselves in definite mathematical ratios is sufficiently startling. What is the explanation? The penetrating intellect of Mendel hit upon the interpretation that is now commonly adopted when he conjectured that segregation results from the purity of the sex cells for the factors that produce one *or* the other member of a pair of contrasted characteristics. The Mendelian characters must be determined by some sort of entities carried by the germ cells, and these entities, whatever they may be, are designated as genes, factors, or sometimes determiners. Mendelian characters go in pairs. Peas are round *or* wrinkled, green *or* yellow, tall *or* dwarfed, etc. In the cross between a green and a yellow pea, for instance, there are genes, or factors, for both green and yellow in all of the cells of the F_1 generation, but when the mature germ cells are produced the factors for green and for yellow, according to Mendel, do not go into the same gamete; they separate so that the factor for yellow goes into one sex cell, and the factor

for green goes into another. In other words, the mature germ cells are pure for either green or yellow, the two kinds of sex cells being produced in equal numbers.

Let us suppose now that the germ cells of an F_1 pea meet at random with those of another individual of the same generation. Obviously, a cell with the factor for green may meet with another cell having the factor for green, or with one having the factor for yellow. Likewise, a cell with the factor for yellow may meet with a cell having a factor for yellow or with one having a factor for green. According to the rules of chance, there will be in the long run

$$1\ YY + 2\ YG + 1\ GG$$

This is precisely the ratio we should get if we were to toss up pairs of pennies and counted the number of times they turned up both heads, both tails, or a head and a tail. In the long run two heads would turn up in one-fourth of the throws, two tails in a fourth, and a head and a tail in half of the throws. Or suppose we were to mix together equal numbers of yellow and green beads and then put the mixed lot into two bags. If we should pick out a bead at random from each bag, our pairs of beads might consist of two yellow beads, two green beads, or one yellow and one green bead. If we drew a large number of pairs in this way we should find that in one-fourth of the pairs the two beads would be yellow, in one-fourth, green, and in one-half of the cases one bead would be yellow and the other green. We may consider that our two bags of mixed beads represent two individuals of the F_1 generation resulting from a cross between a yellow and a green pea, the beads corresponding to the genes for yellow or green in their sex cells; the pairs of beads would then represent the individuals resulting from the union of the sex cells from the two F_1 parents. The fact that we draw out only one bead from each bag corresponds to the production of a gamete pure for the factor of green or yellow, and explains why our resulting pairs of beads occur in a Mendelian ratio.

Mendel's law is based upon the laws of chance. Gametes which are pure for one or the other factor for a Mendelian pair

of characters meet at random and produce all the possible combinations. Mendel's law is the inevitable outcome.

THE DIHYBRID RATIO

Suppose now we cross two varieties, differing in two pairs of characters—say a tall yellow with a dwarf green pea. We obtain in such a case a result which would occur if the factors for tall and dwarf were distributed quite independently of those for yellow and green. The F_1 generation shows the two dominant characters, *i. e.*, it is composed of tall plants with yellow seed. The F_2 generation is composed of several kinds of plants determined by the possible combinations of the sex cells of the F_1. Bearing in mind that the sex cells may contain a factor for only one member of a pair of contrasted characters, the sex cells may carry the following com-

Gametes of F_1

Gametes of F_1	TY	TG	DY	DG
TY	TY TY	TY TG	TY DY	TY DG
TG	TG TY	TG TG	TG DY	TG DG
DY	DY TY	DY TG	DY DY	DY DG
DG	DG TY	DG TG	DG DY	DG DG

Zygotes in squares

Zygotes in squares

FIG. 161—Diagram of the F_2 generation of a cross between a tall yellow and a dwarf green pea.

binations of factors: tall yellow, tall green, dwarf yellow, and dwarf green, the combinations tall dwarf and yellow green being excluded in accordance with the principle of the purity of the gametes for contrasted characters. Each of these four kinds of

sex cells may unite with any of the four others, so that there are sixteen possible combinations. A convenient method of representing these is by the use of a sort of checkerboard of sixteen squares (Fig. 161). Writing the formulas of the sex cells of one parent on the upper side of the checkerboard, and the formulas for the sex cells of the other parent on the left side, we may indicate the possible combinations, or zygotes, in the various squares. It

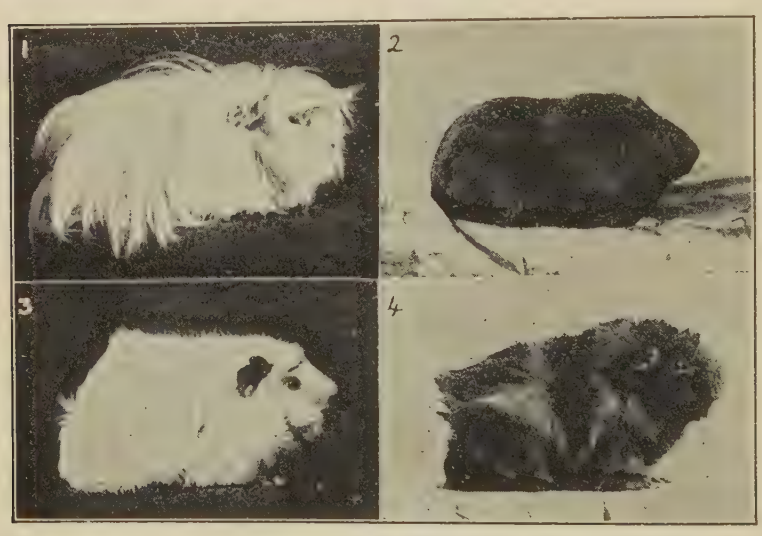

FIG. 162—*1*, A long-haired, rough-haired albino guinea pig pure for these three recessive characters. *2*, a short-haired, smooth-haired red guinea pig homozygous for smooth and red hair, but heterozygous for length of hair, i.e., with long hair recessive. *3*, a short-haired, rough-haired albino guinea pig, son of No. *1* and a red, short- and smooth-coated female heterozygous for albinism, but otherwise pure. The rough hair of *1* is dominant. *4*, a short-haired, rough-haired, red guinea pig, son of No. *1* and a homozygous smooth, short, red-haired female of the same appearance as *2*. (After Castle.)

is obvious that, owing to the principle of dominance, several of the resulting individuals of the F_2 generation will have the same appearance, although possessing a different germinal constitution. Such forms are said to belong to the same phænotype. Individuals having the same genes belong to the same genotype, however they may differ in general appearance. The one term has reference to appearance; the other to hereditary composition.

A study of our checkerboard indicates that there are four phænotypes, and that they occur in the following ratio:

9 tall yellow: 3 tall green: 3 dwarf yellow: 1 dwarf green.

This is the so-called dihybrid ratio, and it is the one typically produced by crossing varieties differing in two pairs of characters. This ratio, like the monohybrid ratio, is due to the laws of chance, and it is brought about by the circumstance that the distribution of one pair of characters occurs in entire independence of the distribution of the other. It exemplifies a principle which has been designated as "the law of the independent assortment of genes." A trihybrid ratio is produced when we combine three independent pairs of characters, and still more complex combinations are possible, although it is difficult to work them out in practice.

CELLULAR BASIS FOR MENDELIAN SEGREGATION

Were we asked why the germ cells are pure for contrasted Mendelian characters we could point to the behavior of the chromosomes in the maturation of the germ cells as providing a very probable and satisfactory answer to the question. It was suspected, long before the resurrection of Mendel's law, that the nucleus of the germ cell plays a very important rôle in hereditary transmission. Hereditary traits are derived to about the same extent from both male and female parents, and the nuclear contributions of both parents to the offspring are also approximately the same. Since the cytoplasm of the egg and sperm differs so enormously in amount, a preponderating rôle in heredity would seem to be played by the nucleus. This conclusion is strengthened by a consideration of the elaborate mechanism of mitosis which divides each chromosome in half during each cell division. It is further strengthened by the reduction of chromosome number that occurs in the maturation divisions of the sex cells preparatory to fertilization. All of these processes seem to be directed toward the preservation of the individuality and number of the chromosomes. What is of especial significance in this connection is that

the facts of chromosome behavior lend themselves very beautifully to the explanation of Mendelian inheritance, provided we make the simple assumption that the distinguishing factor for any given character is carried by a particular chromosome. As we have seen in the chapter on embryonic development, each chromosome in the process of synapsis, which immediately precedes the maturation divisions of the sex cells, pairs with a corresponding, or homologous, chromosome. It should be borne in mind that each individual produced by sexual reproduction has two sets of chromosomes, one from the male and the other from the female parent. These sets remain separate up to the period of sexual maturity when, just before the mature germ cells are formed, the chromosomes come together in pairs, each chromosome derived from the male parent pairing with a homologous chromosome derived from the female parent. The subsequent separation of the members of these homologous pairs in the maturation divisions affords the means of separating the genes, or factors, for the pairs of characters that we find in Mendelian inheritance.

If we suppose that in our example of a cross between a tall green and a dwarf yellow pea, the factors for green and yellow are carried by homologous chromosomes that pair in synapsis, and that similarly the factors for tall and dwarf are carried by another pair whose behavior is quite uninfluenced by the first, then we may understand why the factors for green and yellow never get into the same germ cell. There is nothing to prevent the chromosome with the tall factor going into the same cell as the chromosome for either yellow or green. Likewise the chromosome with the factor for dwarfness may go into the same cell as the factor for yellow or green. In this way we may explain why the germ cells contain only those combinations of factors which we have described, namely, TY, TG, DY, DG.

These genes, or hereditary factors, should not be regarded as solely responsible for the formation of the characters for which they stand. Each character is really the result of a great many factors. Such characters as dwarfness, or wrinkled contour of

seed are attributes rather than things, and if we should consider that a gene produces a character much as a seed produces a particular kind of plant, we should fall into a grave error. Genes obviously have to work in company with others to produce anything at all. A gene could not give rise to a pink eye in a fruit fly unless other factors conspired to produce an eye that could be made pink through the influence of the particular gene in question. *Genes are differential factors.* Alter a gene, and the final outcome is a change which we may designate as a character. A change in a gene commonly produces its most conspicuous effect upon a particular part of the organism, but its influence is often manifested in less obtrusive ways in other parts. On the other hand, changes in different genes may produce much the same effect upon the body. Just how a gene may express itself in the organism is determined by a multitude of influences that shape the course of embryonic development.

THE CLASSES OF VARIATIONS

The progress of genetics has demonstrated the existence of a fundamental distinction between two classes of variations, (1) the somatogenic, those which arise in the body as a result of its activities or the influence of the environment, and (2) the blastogenic, or germinal, which arise in consequence of some change in the germ plasm. Should we develop our muscles by exercise, or become deaf as the result of an attack of scarlet fever, these changes would represent purely somatogenic, or bodily variations. If such bodily changes are hereditary at all, which is doubtful, their effect is relatively slight. On the other hand, the germinal variations are known to be strongly inherited. Of the variations depending upon changes in the germ plasm we should distinguish between (1) those resulting from different combinations of hereditary factors, and (2) those due to a change in the factors themselves. As a result of Mendelian segregation we may obtain a great number of diverse forms, but these are due simply to different combinations of factors already present in the parents. Most variability that arises as a result of crossing is undoubtedly

of this type. It is a kind of variability that may be compared to the different combinations obtained by shuffling and dealing a pack of cards. But in addition to this kind of variability, there are the occasional changes in hereditary factors that correspond to the production of new kinds of cards in the pack. Such variations are much rarer than the ever present somatic modifications, and they are also less frequent than the occurrence of varied Mendelian combinations. Nevertheless, a large number of them have been described. The gardener may detect now and then a plant that stands in marked contrast to the rank and file of his

FIG. 163—The fruit fly *Drosophila melanogaster:* normal male at left, and mutant dichæte at right. (After Morgan.)

other plants. Variations of this type have often been termed "sports," but we should now designate them as mutations. A great many of such sudden and distinct variations have been found to breed true, and they have therefore formed the starting point of new varieties. In this manner have arisen the navel orange, runnerless strawberries, nectarines from peaches, and numerous varieties of grains, fruits, and cultivated flowers. The fruit fly Drosophila has produced more than 400 mutations during the twenty-five years in which it has been under careful observation. These mutations affect eye color, body color, size, shape and venation of wings, number of bristles—in fact practically all parts of the body. All of these variations are transmitted according to Mendel's law, most of them being recessive, although a few are dominant, and others are partly dominant. Drosophila

has proven to be a wonderfully favorable form for the study of heredity and variation. One needs only a few suitable bottles and a bit of banana to supply food for the larvæ in order to rear large numbers of individuals, and, as it takes only about three weeks for the flies to become mature, many generations can be raised in a short time. The remarkable insight into the mechanism of Mendelian heredity that has been attained by Dr. T. H. Morgan and his associates in their work on this form has been made possible through the circumstances to which we have alluded. But Drosophila has proven to be a favorable form for another and quite different reason. It contains a small number (eight) of chromosomes, some of which are easily recognizable by their size and form. There are, therefore, only four chromosomes in the mature germ cells.

LINKAGE AND CROSSING OVER

In our exposition of the probable cytological basis of Mendelian inheritance we assumed that the independent assortment of hereditary characters was due to the independent distribution of chromosomes. But in Drosophila there are over 400 Mendelian characters, and only four pairs of chromosomes; consequently we should expect that, in accordance with the theory, each chromosome would carry many hereditary factors. If this were true, we should expect that the characters would be inherited in groups. This in fact has been found to be the case. Characters that tend to be inherited together are said to be linked. Now it is a very significant fact that in Drosophila all the hereditary characters thus far known fall into just four linkage groups, which is the same number as there are chromosomes in the mature germ cells. It is not likely that this is a purely fortuitous coincidence, and this conclusion is supported also by a considerable amount of independent evidence. There is one large group of characters associated with sex, and it seems probable that the factors for these are carried in the large sex chromosome. There is one very small group of characters (only four), and it is tempting to suppose that the factors for this group are carried by the

very small fourth chromosome. Finally, there are two relatively large groups of characters belonging probably to the two fairly large second and third chromosomes. Linkage has been observed in sweet peas, corn, grasshoppers, and several other forms, but, owing to the larger number of chromosomes in most species, the phenomena of linkage are known far less thoroughly than in the fruit fly.

One striking peculiarity of linkage in Drosophila is that it is not complete. Characters tend to be inherited together in dif-

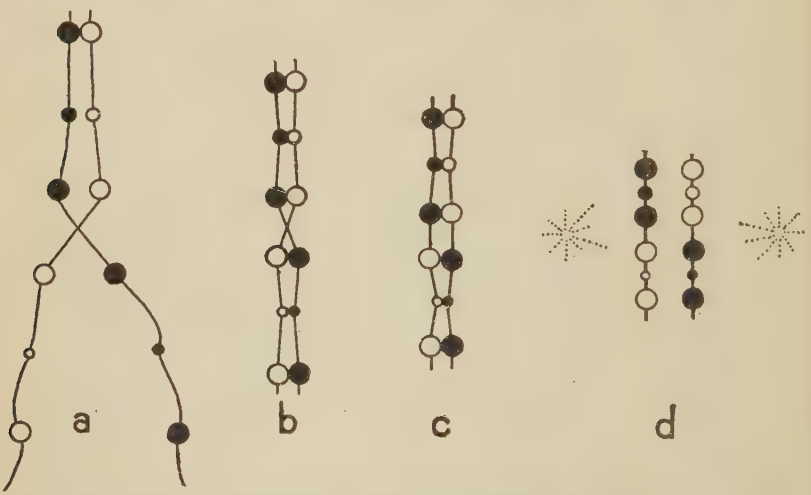

FIG. 164—Diagram to illustrate the theory of crossing over: *a*, *b*, chromosomes twisted about each other; *c*, *d*, the chromosomes separating after being broken apart at the point of crossing. Some of the factors (represented by circles) originally in one chromosome are now in the other. (After Morgan.)

ferent degrees. This variation in linkage has been plausibly explained by Morgan on the theory that (1) the genes, or factors, for linked characters are arranged in a linear series in a given chromosome; (2) that the chromosomes twist about each other in synapsis, and (3) that when they separate in reduction they break apart so that a part originally in one chromosome comes to be associated with its synaptic mate. There is supposed to be an exchange of parts, or a "crossing over," which involves whole sections of chromosomes. If now two factors lie very close to-

gether in a chromosome it is not likely that a break will occur between them; their characters will be closely linked. If factors are far apart they are much more apt to be separated; consequently their characters will be loosely linked.

It is not possible to give here an adequate presentation of all the evidence favoring this view. This evidence is set forth at length in Morgan's *Physical Basis of Heredity* and in many special papers, and it is of a character that has convinced most critical and skeptically minded workers in genetics that the theory is very probable. The conclusion to which the work on Drosophila and other experimental investigations seem to point, is that mutations are due to some changes in small parts of chromosomes representing hereditary factors. These mutations, therefore, obey Mendel's law of heredity. Apparently they depend upon discrete, if small, transformations, probably of a chemical nature, in a single unit of the substance of a chromosome. At any rate, they are relatively stable changes, although each gene may in course of time mutate into something that has a little different effect upon the development of the organism, producing thereby a new, so-called "unit character."

FIG. 165—Results of crossing varieties of corn differing in the color and fullness of the kernels. The ear to the left is the result of crossing a double recessive colorless, shrunken corn with a hybrid between a white, shrunken and a colored, non-shrunken corn. The ear to the right is the result of crossing a white, shrunken corn with a hybrid between a white non-shrunken and a colored, shrunken corn. In the ear to the left most of the full kernels are colored and most of the white ones shrunken. In the ear to the right most of the full kernels are white and most of the colored ones shrunken. These relations indicate linkage between the factors for color and fullness of the kernels. (After Hutchison.)

Why these mutations arise in Drosophila is quite unknown. Efforts to produce them in greater frequency through the application of strong environmental stimuli continued over many successive generations have produced no appreciable

effect. In other forms, there is some indication that environmental agencies have produced changes in the germ plasm that have resulted in heritable variations, but while it seems probable *a priori* that variability may be brought about in this way, our knowledge of the actual causes of mutations is exceedingly slight.

HEREDITY AND SEX

It was inevitable that the rediscovery of Mendel's law should stimulate inquiry as to the possible relation of Mendelian inheritance to the determination of sex. What decides whether a given fertilized egg develops into a male or a female is a problem which has occasioned much speculation ever since the time of the ancient Greeks. Nutrition, relative age or vigor of parents, the time at which the egg is fertilized, and many other causes, have been advanced as affording solutions of this problem, only to be discarded as inadequate. According to Thomson, Drelincourt, in the eighteenth century, brought together 262 groundless theories of sex, and Blumenbach caustically remarked that it was certain that Drelincourt's own theory formed the two hundred and sixty-third. A promising basis for the final solution of this long standing problem seemed at last to be afforded by some observations on the spermatogenesis of insects. In 1891 Henking discovered in the spermatogenesis of a species of bug that there was a large odd chromosome which was not distributed like the others, but passed during one of the divisions of the spermatocytes into one or the other of the two daughter cells. This observation was confirmed by several other investigators, one of whom, Dr. C. E. McClung, advanced the view that the accessory, or X chromosome, as it was termed, is a determinant of sex. It was soon ascertained by Professor E. B. Wilson that in many insects the males have one less chromosome in the sex and body cells than the females. This is due to the fact that there is one X chromosome in the male and two X chromosomes in the female. Moreover, the mature eggs of these females all contain one X chromosome, whereas one-half of the sperm cells of the male contain an X chromosome and the other half do not.

This dimorphism among the spermatozoa affords a means of producing the two sexes. All of the studies referred to point to the conclusion that if an egg is fertilized by a sperm containing an X chromosome it develops into a female, and that if it is fertilized by a sperm devoid of an X chromosome it develops into a male.

FIG. 166—Chromosomes of the sex cells of the bug *Anasa tristis: a*, chromosomes of the first spermatocyte seen from a polar view; *b*, division of second spermatocyte; *c*, *d*, polar views of the two sets of chromosomes seen in *b*; *e*, chromosomes of the spermatogonia; *f*, the same arranged in pairs with the exception of the odd sex chromosome, *h*; *g*, chromosomes of the oögonia; *h*, the same arranged in pairs and showing the two sex chromosomes in the female; *h*, sex chromosomes; *l*, a large chromosome, but not a sex chromosome; *m*, a very small chromosome. (After Wilson.)

In many species the X chromosome of the male has a somewhat smaller mate known as the Y chromosome. In these cases a male is produced when an egg is fertilized by a Y-containing sperm cell. Such males are therefore XY in composition instead of XO. It is the dimorphism of the sperms in any case that effects the determination of sex.

It has now been ascertained that a large number of organisms exhibit differences in their chromosome complex characteristic of the two sexes. In most forms, the sperms are dimorphic, or in other words, the males are heterozygous for the factors which determine sex. There are relatively fewer forms, such as the birds and the Lepidoptera (butterflies and moths), in which the females are heterozygous, and in which there are male-producing and female-producing eggs. The mammals, so far as known, the insects other than the Lepidoptera, and most other groups of the animal kingdom whose sex chromosomes have been studied, belong to the first group. Man, who has forty-eight chromosomes, according to Painter, shows the usual X and Y types of spermatozoa.

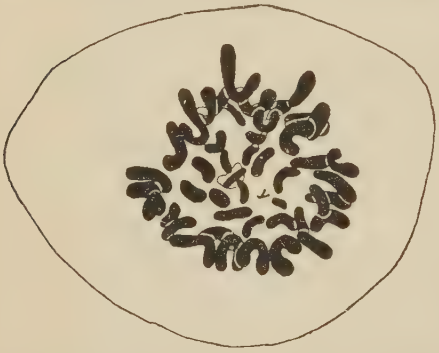

FIG. 167—Chromosomes of human spermatogonia (there are forty-eight chromosomes in the figure): *y*, the Y chromosome, the X chromosome not being easily distinguishable from the others. (After Painter.)

Other things equal, we should expect that, in accordance with the chromosome theory, the two sexes would be produced in approximately equal numbers. Nevertheless, we find that in many species there are consistent departures from equality of sex ratios, and in a few cases these departures are quite extensive. In man the sex ratio at birth is about 105-106 males to 100 females. There is good evidence that in some forms the proportions of the sexes may be modified by environmental factors. These facts, however, are not inconsistent with the chromosome theory, nor do they indicate that the sex of an embryo can usually be changed after the egg is fertilized. Departures from equality may result from the fact that members of one sex die more frequently than those of the other sex. Possibly also the two types of spermatozoa may not be equally successful in fertilizing the eggs. Careful

measurement of the lengths of the heads of sperm cells in several species of animals have shown that the sperms tend to fall into two classes on the basis of head size. These differences may well affect the rapidity of movement, or the readiness with which the sperm head penetrates the egg cytoplasm.

It is at least uncommon for the sex of an organism to be changed after fertilization has been effected. There are, however, a few well authenticated instances of change of sex in birds, mainly in pigeons and in domestic fowls. Crew has reported the case of a hen that laid fertile eggs and afterward took on the plumage and characteristic behavior of a rooster. The bird subsequently became the father of young chicks. Upon post-mortem examination it was discovered that the ovary had become almost completely destroyed as a result of tuberculosis, and that there had developed in its stead a testis which was shown to produce typical spermatozoa.[1] The higher animals rarely have the experience of being at one time female and at another time male, but it may be recalled that some of the lower animals (the protandrous hermaphrodites) normally first produce sperm cells and afterward lay eggs. We should perhaps regard the sex chromosomes as containing factors which may turn the balance between male-producing and female-producing tendencies in the one or the other direction. They are not the *sole* determinants of sex. Like other Mendelian units, sex factors are differential factors, and at times other forces outweigh their influence. Every embryo apparently has the potency of producing to a greater or less degree the characteristics of both sexes. In those curious anomalies known as intersexes one may find all gradations between males and females. A mild degree of intersexuality may characterize a great many individuals without being sufficiently pronounced to become abnormal. Sex is probably determined by the relative potency of factors which are carried in the inheritance of both males and females.

It is a significant fact that the unfertilized egg of the queen

[1] A very similar case of change of sex in pigeons has been described by Dr. Riddle.

bee gives rise to a male. The inheritance of the male sex in this case comes entirely from the mother. Should the germ plasm from the male be added to the egg through fertilization the result would be a female. The larger amount of chromatin in the fertilized egg is apparently the cause of the development of the female sex.

The chromosome mechanism which is normally effective in the determination of sex affords a clue to a peculiar type of

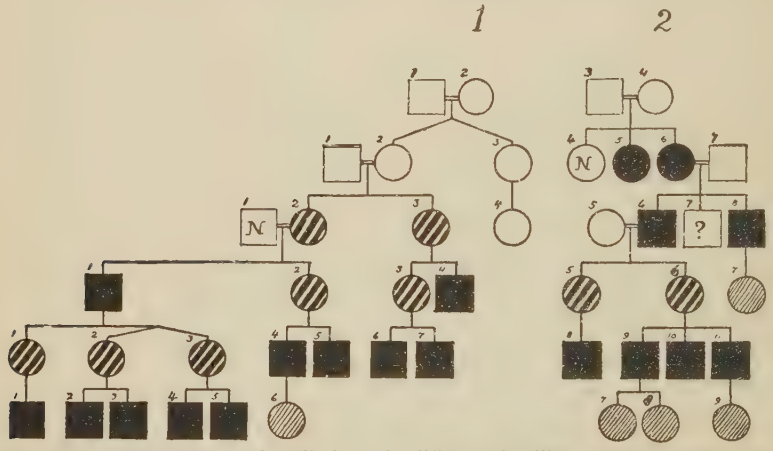

FIG. 168—Inheritance of color-blindness in different families. Males represented by squares, females by circles; color-blind individuals in black; carriers designated by stripes; and women supposed to be carriers by shaded circles; normal individuals designated by *N*, and those about whom nothing is known by empty squares or circles or by a question mark (?). (After Bowditch.)

hereditary transmission known as sex-linked inheritance. There are certain defects, such as color-blindness and hæmophilia (bleeding), which are rarely found in women, but which women may transmit to their sons. A color-blind man marrying a normal woman produces offspring all of whom at least appear to be normal, and the sons really are so. The daughters, although appearing normal, are nevertheless carriers of the defect, *i. e.*, they are heterozygous for color-blindness. The character is recessive, and it is apparently prevented from becoming manifest on account of the opposing influence of a corresponding factor for the normal condition. If one of the daughters marries, half of her sons may

be expected to develop color-blindness, the other half being normal. Half of her daughters will be carriers. Should a daughter who is a carrier marry a color-blind man, half of her sons will be color-blind, and half will be normal; half of her daughters will be carriers, and the other half will be color-blind. Color-blindness is rare in females because it requires a double dose of the factor to produce this effect, while only a single dose suffices to make a color-blind male.

We may readily understand this curious mode of transmission if we make the simple assumption that the factor for color-blindness is carried by the sex chromosome. In the male there is only one X chromosome, and if this contains the factor for color-blindness there is no opposed factor to prevent its manifestation. If a color-blind male marries a normal female he contributes an X chromosome to the germ plasm of all of his daughters, but his Y chromosomes go to his sons, who therefore do not inherit this trait. The X chromosome of male offspring is derived from the mother. Consequently, if the mother is heterozygous for color-blindness, *i. e.*, if one of her X chromosomes contains the factor for this defect and the other does not, half of her sons will be color-blind.

Sex-linked inheritance has been found in several species of animals and in a few plants. There are more than 100 sex linked characters in Drosophila and they are transmitted according to the scheme just described. In the birds and the Lepidoptera, in which the females are heterozygous for sex-determining factors, the behavior of sex-linked characters is, as we should expect, just the reverse of what it is in man and Drosophila.

The insight which has been gained during the last quarter-century into the determination of sex has shown that sex is a Mendelian character dependent upon the same chromosomal mechanism that determines other Mendelian characters. The relatively constant numerical proportions of the sexes rests upon the same fundamental basis that determines the mathematical ratios observed in Mendelian segregation in general. The heredity of

sex and sex-linked characters constitute only a special form of Mendelian heredity.

THE INTERACTIONS OF HEREDITARY FACTORS

Mendelian inheritance is manifested in a variety of ratios due to the different ways in which factors interact in the production of visible characteristics. Complete dominance is by no means

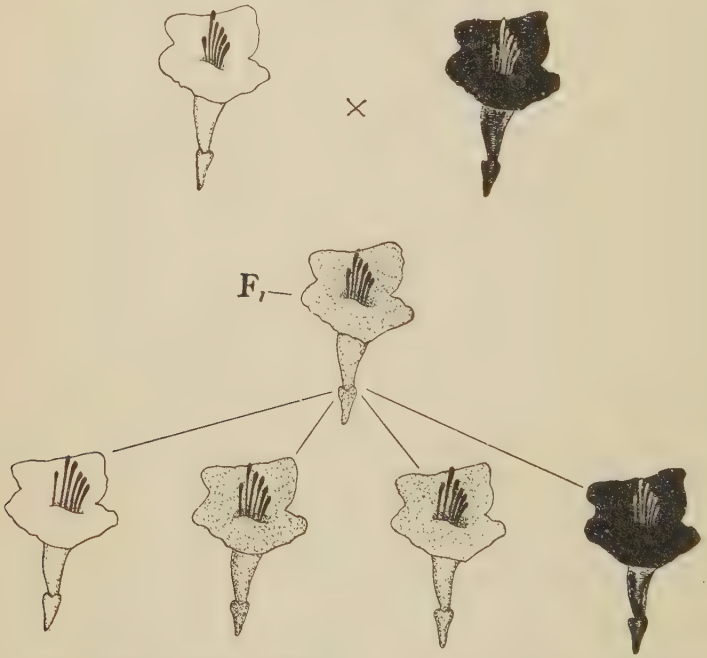

FIG. 169—Results of crossing a white and a red variety of four o'clock, *Mirabilis jalapa*. The red parent in the upper line is represented in black and the stippled flowers are pink. F_1, the first generation. The pink F_1 produces one white, two pink, and one red, as shown in the lower row. (After Correns.)

a general phenomenon, and there are many cases in which the F_1 is intermediate between the parental types. A cross between a red and a white four o'clock produces pink offspring, owing to the incomplete dominance of red over white. The F_2 generation consists of one-fourth pure-breeding reds, one-half heterozygous pinks, and one-fourth pure-breeding whites. Sometimes factors

interact so as to give rise to a new character. Such a case is afforded by the breeding of the Andalusian fowl. Breeders have long endeavored to obtain a variety of Andalusians which would breed true to type, but in vain. In addition to producing their own kind with its characteristic bluish color, the Andalusians always give rise to a certain number of black and splashed white progeny. If, however, the black and the splashed whites are crossed, all their progeny are Andalusians. When the breeding of these fowl was tested in the light of Mendel's law it was discovered that the blue fowl produced three types in the ratio of 1 black; 2 blue Andalusians: 1 splashed white.

The explanation of the instability of the blue Andalusians is that they are heterozygous. They behave like the pink four o'clocks which produce reds and whites in addition to pink flowers. The factors for black and white conspire, for some reason, to produce a blue color as the result of their interaction.

The interaction of factors plays an important part in the inheritance of color in many different types of organisms. A striking instance of this is afforded by crossing two slightly different strains of white sweet peas of the Emily Henderson variety. The chief visible difference between these two strains is that in the one the pollen grains are oblong, while in the other they are round. When these two white strains were crossed their progeny were found to be of a purple color very much like that of

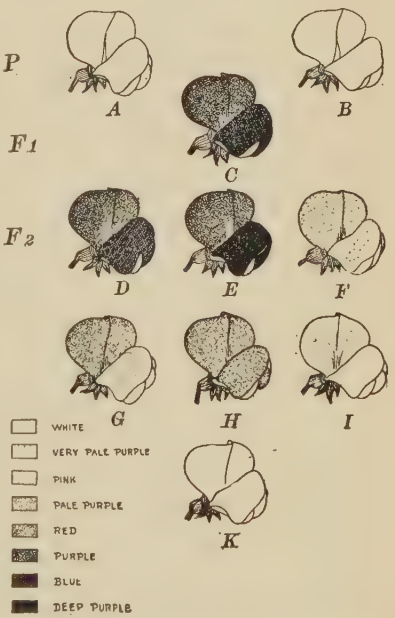

FIG. 170—The results of crossing two white strains of the Emily Henderson variety of sweet peas: *P*, parents, *A*, *B*; *C*, colored pea of the F_1 generation; *D*-*K*, different colored types in the F_2 generation. (From Conklin, after Punnett.)

the wild Sicilian pea from which our numerous cultivated varieties have been derived. The generally accepted explanation of this curious result is that color is a product of two factors, a color determiner C, and a factor for pigment which we may designate by P. Where either of these is absent the flower is white. The factors C and P are called complementary, since each supplies what is lacking in the other to produce the character in question. The two strains of white peas are supposed to be white for different reasons, the one lacking the C factor and the other lacking the P factor. When the varieties are crossed these two complementary factors are brought together in the F_1 and a colored flower is the result.

The production of a flower similar to the ancestral Sicilian pea as a result of this cross affords a typical instance of what is commonly called reversion, or atavism. It has long been recognized that organisms occasionally appear which closely resemble some remote ancestor. Darwin observed that reversion frequently followed upon the crossing of distinct varieties, but he had no adequate explanation of the phenomenon. The inheritance of a remote ancestor was supposed to be carried in a dormant state until conditions, connected somehow with the mingling of different bloods, brought the ancient inheritance to expression. Mendel's law has thrown a flood of light upon the subject of reversion, as it has upon other phenomena of inheritance. Reversion is commonly brought about by the restoration of the full complement of factors possessed by some ancestor.

Varieties have frequently arisen through factors mutating into a modified form which is recessive to the normal type. Some geneticists have interpreted such variations as due to the loss of factors, but while this theory, which is known as the presence-absence theory, has the merit of simplicity and more or less plausibility, it is not in accord with many of the facts of heredity. The manifold variety of sweet peas, according to this theory, is the result of the loss, now of this factor and now of that. The two strains of white peas we have considered are regarded as due to the loss of different factors, and when they are crossed all

of the color factors present in the ancestral species are restored, and hence there is a reversion in the progeny. We need not suppose, however, that factors have actually been lost. If we assume that they have been simply changed so that they do not have the same influence on development, the facts of reversion are accounted for equally well, and we avoid many of the difficulties into which the presence-absence theory leads us.

It not infrequently happens that in breeding different-colored varieties of mice, rabbits, and guinea pigs, we obtain progeny of the gray, or agouti color characteristic of the wild ancestral species of these animals. Crossing certain varieties of black and yellow rabbits, blacks and albinos, or yellows and albinos, has been found to produce gray rabbits in the F_1 generation. In mammals many factors are involved in the production of color. Of fundamental importance is a general color determiner C which is necessary if any pigment is developed at all. The absence of this factor produces albinism which is characterized by white hair and pink eyes, the latter being due to absence of pigment in the iris. An albino may carry all other kinds of color factors, but if the C factor is not functional no pigment is formed. Gray, or agouti is produced by a factor which causes the dark color of the hair to be interrupted by a light band, and it is accordingly spoken of as a barring, or ticking factor. A rabbit without this factor will usually be black, although if it has no black factor, it will be of some lighter shade. Absence of factors for darker pigments may result in yellow or some relatively light color. Suppose we cross an ordinary yellow rabbit with an albino having the factors for dark pigments and also the agouti factor. As the C factor is brought in by the yellow rabbit, and the other components of gray are furnished by the albino, we have gray color in the progeny, and hence a case of reversion by restoration to the ancestral wild type.

It is possible to test out this interpretation of reversion by various kinds of experimental matings, and the general theory has been borne out by a large amount of carefully conducted investigations. In Mendelian analysis it is fortunately possible

to put theories to the test by devising the proper experiments and then observing if the results conform to theoretical expectations. If they do not, other theoretical formulations are adopted until one is finally found which fits all the facts.

Reversions may be caused in a somewhat different manner by the reappearance of old recessive traits. Should two forms mate which are heterozygous for a recessive character, the latter would be expected to appear in one-fourth of the offspring. Traits may be carried in the germ plasm without noticeable modification for a great many generations. There is no evidence that genes are changed by the different associations in which they take part.

It sometimes happens that two or more factors produce much the same effect. One such instance was discovered by Nilsson-Ehle in crossing a particular variety of black oats with a variety of white oats. The dark color proved to be dominant, but the second generation was found to consist of fifteen blacks to one white, instead of the usual 3 to 1 ratio. The 15 to 1 ratio is readily explicable as a dihybrid ratio produced by two independent factors for black. Suppose we designate these as B_1 and B_2, and the corresponding factors in the white variety as b_1 and b_2. The composition of the F_1 would be $B_1\ B_2\ b_1\ b_2$. The germ cells of this F_1 would therefore be $B_1\ B_2$, $B_1\ b_2$, $b_1\ B_2$, $b_1\ b_2$, and their possible combinations may be represented in the following diagram (Fig. 171). It will be seen that all of the zygotes but one—namely $b_1\ b_1\ b_2\ b_2$—will contain at least one factor for black; hence the 15:1 ratio.

Nilsson-Ehle also found a variety of red wheat which, when crossed with the ordinary white variety, gave in the F_2 a ratio of 63 red to 1 white. Here it is probable that there are three independent factors for red, and that the ratio obtained is a modification of the trihybrid ratio, all but one of the 64 combinations of gametes containing at least one factor for red. The several components of characters such as these are known as multiple factors, and their behavior in these instances indicates that they are carried by separate chromosomes.

In some cases the effect of multiple factors is cumulative, *i. e.*, the larger the number of such factors the greater the effect. Should six factors for redness in the cross of red and white wheats produce the maximum color, and should the other zygotes exhibit degrees of redness that vary with the number of factors for this color, the second generation of this cross would exhibit several grades of colors between the red and the white of the original parents. If the intensity of color was also subject to

	$B_1\ B_2$	$B_1\ b_2$	$b_1\ B_2$	$b_1\ b_2$
$B_1\ B_2$	$B_1\ B_2$ $B_1\ B_2$	$B_1\ B_2$ $B_1\ b_2$	$B_1\ B_2$ $b_1\ B_2$	$B_1\ B_2$ $b_1\ b_2$
$B_1\ b_2$	$B_1\ B_2$ $B_1\ b_2$	$B_1\ b_2$ $B_1\ b_2$	$b_1\ B_2$ $B_1\ b_2$	$b_1\ b_2$ $B_1\ b_2$
$b_1\ B_2$	$B_1\ B_2$ $b_1\ B_2$	$B_1\ b_2$ $b_1\ B_2$	$b_1\ B_2$ $b_1\ B_2$	$b_1\ b_2$ $b_1\ B_2$
$b_1\ b_2$	$B_1\ B_2$ $b_1\ b_2$	$B_1\ b_2$ $b_1\ b_2$	$b_1\ B_2$ $b_1\ b_2$	$b_1\ b_2$ $b_1\ b_2$

FIG. 171 —Diagram of the results of crossing two varieties of oats having two independent pairs of factors for color. All of the sixteen zygotes but one (b_1, b , b_1, b_2,) have at least one factor for black, hence the ratio fifteen black to one white.

more or less somatic variability owing to the influences of the environment, one might discover all possible gradations of color between the red and white varieties.

These considerations naturally lead us to the subject of so-called blending inheritance, a phenonemon which at first seemed to stand in irreconcilable contrast to Mendelian segregation. There are several cases in which a character intermediate between those of the parents was found to persist in subsequent generations. Such cases afford a marked contrast to those instances of imperfect dominance which, like the pink four o'clocks, show a typical segregation in the second generation of

hybrids. In crosses between long-eared and short-eared rabbits, for instance, it was found by Castle and his collaborators that the progeny showed a persistent intermediate ear length in the second and subsequent generations of progeny. When the F_1 was crossed back to the parental types a similar intermediate ear length was produced. Similar phenomena have been observed in studying the inheritance of size. A more familiar illustration of blending is found in the skin color of mulattoes which, as is well known, is transmitted to subsequent generations as a more or less intermediate shade between white and black.

Do these apparently stable blends represent a type of inheritance radically different from Mendelian segregation? Apparently they do, but, as East and Lang have pointed out, if a character is the product of a considerable number of factors, there will be an appearance of blending, although each pair of genes involved may segregate in strict accordance with Mendel's law. In the trihybrid ratio formed by crossing red and white varieties of wheat, any one parental type is found in only one out of 64 individuals of the F_2 generation. Were four pairs of factors involved, the parental types would recur only once out of 256 cases, and if there were six pairs of factors, only once out of 4096 cases. With a large number of factors a relatively large part of the progeny would be close to the intermediate condition, and in practice the original parental characters would not ordinarily be met with at all.

Such, in brief, is the multiple factor theory of blending inheritance. This theory is in entire accord with what is known of the mechanism of hereditary transmission; and it enables us to interpret inheritance in general as essentially Mendelian. It is also supported by the fact that the variability of the second generation of blends is generally greater than that of the first, thus indicating the existence of segregation of factors. A study of the families of mulatto parents frequently shows that there is a striking variety in the skin color of the children.

Breeders of plants and animals have long been concerned over the influence of inbreeding and crossbreeding. It is com-

monly believed that inbreeding results in deterioration, while the mingling of the germ plasms of somewhat different stocks (providing they are not too different) enhances the vigor of the progeny. There are many facts which seem to support both of these conclusions. Inbreeding in corn, for instance, is usually followed by a marked diminution of yield. Close inbreeding in animals has often been found to produce inferior progeny. There are many records of cousin marriages which resulted in imbecile, epileptic, or otherwise defective children, although the parents themselves manifested none of these traits. During the Christian era marriage of near relatives and sometimes of remote relatives has long been prohibited

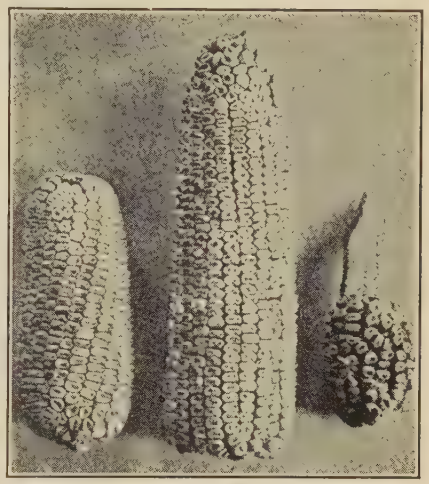

FIG. 172—Results of crossing two strains of Leaming Dent strains of corn (No. 9 and No. 12) inbred for four years. The parent strains at the right and left, the F_1 in the center. (After East and Hays.)

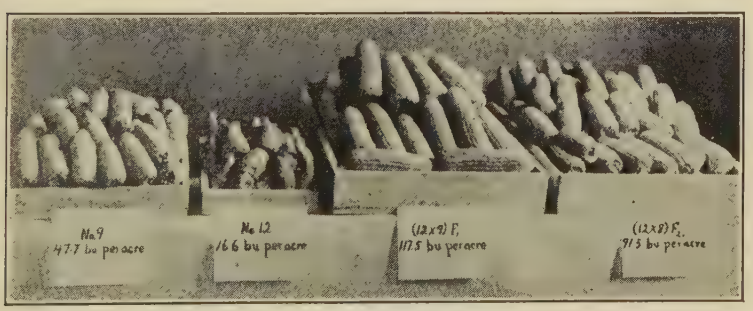

FIG. 173—Yield of inbred strains of Leaming Dent corn (No. 9 and No. 12) as compared with the yield of the F_1 and F_2 generations. Parent strains at left; F_1 and F_2 at right. (After East and Hays.)

in many countries, and about half of the states of the United States now forbid the marriage of first cousins.

But along with many indications of injurious effects that follow inbreeding, we meet with numerous instances in which inbreeding has been followed by no bad results. Many kinds of plants are normally self-fertilizing and are hence subjected to the closest kind of inbreeding. Nevertheless, they thrive as well as many others. Drosophila has been inbred by brother and sister matings for 59 generations without loss of vigor or fertility. The most thorough investigation of inbreeding in higher animals has been carried on by Miss Helen Dean King who has inbred albino rats by brother and sister matings for more than 50 generations. The animals are still healthy and fertile. Early in the course of Miss King's experiments some of the lines exhibited signs of deterioration, but by selecting the more vigorous animals a stable strain was produced which showed no further indications of degeneracy.

The varied results of inbreeding seem to present us with a somewhat paradoxical situation, but it is one which is rendered much less confusing when we interpret the facts in the light of Mendel's law. Most geneticists now hold that inbreeding in itself is not injurious; it is injurious only when the factors for defects are already present in the stock. If a strain were heterozygous for albinism, for instance, this defect would appear only when two individuals carrying a factor for it happen to mate. Then the trait would be expected to crop out in one-fourth of their offspring. Feeble-mindedness, insanity, deafness, and other defects are found in inbred stocks, not because inbreeding produces these traits, but because it makes them appear if the factors for them are already in the germ plasm.

If this is a true interpretation, it follows that if the stock is sound, inbreeding may be carried on with no bad results. In fact, it may prove a real advantage, because it conserves any valuable qualities which the stock may possess, instead of allowing them to become dissipated. There are many inbred families who exhibit a high degree of physical and mental vigor. In the Bach family, the Kembles, and many notable families of Puritan stock, there was a good deal of close intermarriage

whose only result seemed to be the conservation of a superior inheritance. One of the most striking instances of a successful cousin marriage is found in the Darwin family. Charles Darwin married his first cousin, Emma Wedgwood, the granddaughter of Josiah Wedgwood, F.R.S., the founder of the pottery works which make the well known ware that bears his name. Charles Darwin's father, also a Fellow of the Royal Society, was a very able physician, and his grandfather, Erasmus Darwin, F.R.S., also a physician, was noted also as a poet and a man of science. Four of Charles Darwin's sons became noted for their achievements, and three of them attained the high honor of being elected Fellows of the Royal Society. In these sons there converged streams of hereditary influence transmitted by father and mother from an exceptional ancestry. Where there is a real aristocracy of talent and no hereditary defects which threaten to be visited upon the offspring, the intermarriage of relatives may result in great benefit to the race.

For many people the question, Shall I marry my cousin? is one which may come with peculiar poignancy. To all such anxious souls the geneticist must utter a warning, should their ancestry give evidence of hereditary defects. Those of sound and superior inheritance he has no reason to dissuade from contracting a consanguineous marriage. He cannot give an absolute assurance that some undesirable character may not come to light, but the same misfortune might follow any kind of mating whatsoever.

LAWS OF ANCESTRAL INHERITANCE AND FILIAL REGRESSION

Before the great discovery of Mendel became generally known, Francis Galton announced two principles, called the law of ancestral inheritance and the law of filial regression. According to the first of these, an individual inherits, on the average, one-half its qualities from its parents, one-fourth from its grandparents, one-eighth from its great-grandparents, and so on—the series $^1/_2 + {}^1/_4 + {}^1/_8 + {}^1/_{16} + {}^1/_{32} \ldots$ carried out to infinity being equal to unity, or the total heritage. Any one individual, of course, does not inherit from its ancestors in just these pro-

portions. The law purports to express what is true on the average. Oliver Wendell Holmes has remarked that we are omnibuses in which all of our ancestors ride. It is true that we carry the contributions of many ancestors in our germ plasm, but the number represented is not indefinitely large, and it is probable that it does not increase with successive generations. In other words, the omnibus is one of strictly limited capacity, and as more people get in, others get out. Ancestors are lost by wholesale in the reducing divisions of the germ cells. If the individuality of our chromosomes were strictly preserved, we should have room for the heritage of only forty-eight ancestors in our germ plasm. Owing to the possible occurrence of crossing over, however, the number of possible ancestral heritages is greatly increased, but to what an extent cannot be ascertained.

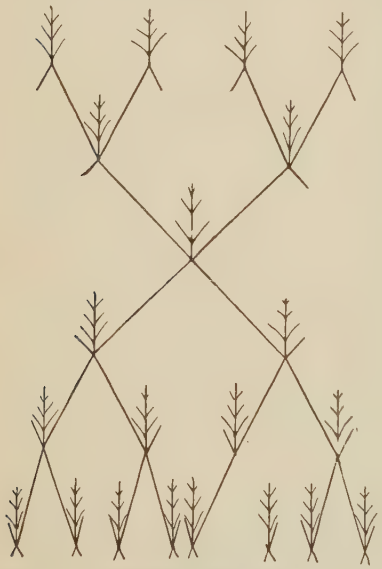

Fig. 174—Diagram illustrating the confluence and separation of strains of hereditary influence, the straight lines indicating the continuous germ plasm from which individuals (rising from the meeting points) take their origin.

The law of filial regression is to the effect that the offspring of parents that deviate widely from the average character of their group are, on the whole, less widely divergent than their parents. In other words, the offspring show a regression toward the mean of the species. Children of very tall parents may be taller than the average, but they are nearer the average type than their parents are. Likewise, the children of very short parents are apt to be somewhere between the height of their parents and the height of the average man. Heredity, according to this principle, tends to pull offspring back towards mediocrity, and this is due to the fact that ancestral inheritance is apt to be average inheritance.

The law of filial regression was based upon a statistical study of many facts of observation. But the principles of Mendelian inheritance preclude our adopting the interpretation of it given by Galton. An albino with pigmented ancestors does not revert toward the average color of its species. Extreme forms are often extreme because they represent an exceptional degree of fluctuating or, somatic variability combined with a marked germinal variation in the same direction. As the somatic modifications are not transmitted to a marked extent, if at all, the offspring would probably exhibit a somatic character not far from the average that would be expected from its hereditary composition. Hence there would be more or less reversion toward the general mean.

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CHAPTER XV

HEREDITY AND ENVIRONMENT

A perennial and much discussed question concerning heredity is whether or not characters acquired by an organism may be passed on to its descendants. Organisms are continually acquiring characteristics of one kind or another as a result of their own activities or the influence of environmental changes. If we expose ourselves to the sun we are apt to acquire sunburn or freckles, and if we engage in severe manual labor the skin of our hands becomes thickened, or calloused. These modifications are typical illustrations of acquired characters as contrasted with germinal characters, such as blue or brown eyes, which depend upon the constitution of the germ plasm. It is well known that germinal variations, like albinism or supernumerary fingers, may be transmitted to subsequent generations. A few decades ago it was generally held that acquired characters were also transmitted. Usually, in fact, no distinction was made between germinal and somatic modifications. There seemed to be no reason why any kind of character might not be inherited as well as any other.

The doctrine of the transmission of acquired characters was brought into especial prominence by the great French naturalist Lamarck, who was one of the most distinguished of the pre-Darwinian proponents of the theory of organic evolution. According to Lamarck the transmission of acquired characters is the chief cause of evolutionary changes. It must be conceded that there are many features of structure and behavior which may be very plausibly explained if acquired modifications are passed on by inheritance. The soles of our feet, for instance, are relatively thicker than the rest of the skin and their increased thickness is manifested even in the embryo. Since walking

upon the ground causes the soles of the feet to become thicker we need only assume that this modification is hereditary in order to account for the fact that we are already equipped at birth with thickened soles. The Lamarckian theory seems also to afford a reasonable explanation of rudimentary organs. Inasmuch as the disuse of organs frequently causes them to diminish in size, the cumulative hereditary effects of disuse would, in time, lead the organs to become rudimentary and eventually to disappear. The numerous blind species of cave animals with rudimentary eyes are often cited as evidence for the inherited effect of disuse.

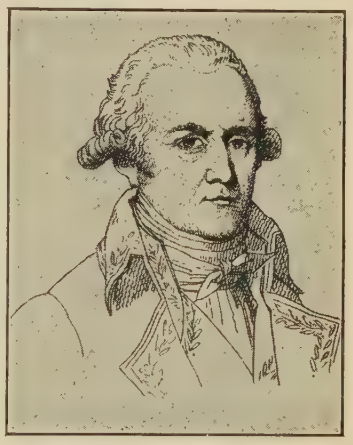

FIG. 175—Lamarck.

The inheritance of acquired characters, or the Lamarckian factor, as it is often called, was accepted by Charles Darwin and most of the earlier advocates of the theory of evolution. Lamarck had no theory as to why acquired characteristics come to be inherited, but Darwin was strongly impressed with the importance of gaining some insight into the causal mechanism of heredity and variation, and, as a step in that direction, he propounded his provisional theory of pangenesis. As Darwin was something of a Lamarckian as well as a Darwinian, he naturally held that one of the requirements of an adequate theory of heredity was that it should give a plausible explanation of the transmission of acquired characters, and his theory seems especially designed for this purpose. The fundamental assumption is that the various cells of the body give off into the blood or other fluids very minute living units called gemmules, and that the gemmules come to be stored in the germ cells, which are supposed to have a special affinity for attracting these bodies. When the germ cells give rise to a new individual, the gemmules,

which are assumed to be of many different varieties, are supposed to produce each its own kind of organ. Each part of the offspring was thus held to be derived from the corresponding part of the bodies of the parents. Should an organ be increased in size through frequent use, it would, according to Darwin, produce more gemmules. More gemmules would therefore be stored in the germ cells, and hence the resulting individual would have the corresponding organ more fully developed.

Granted the premises of the theory, the transmission of acquired characters is readily accounted for. The theory is

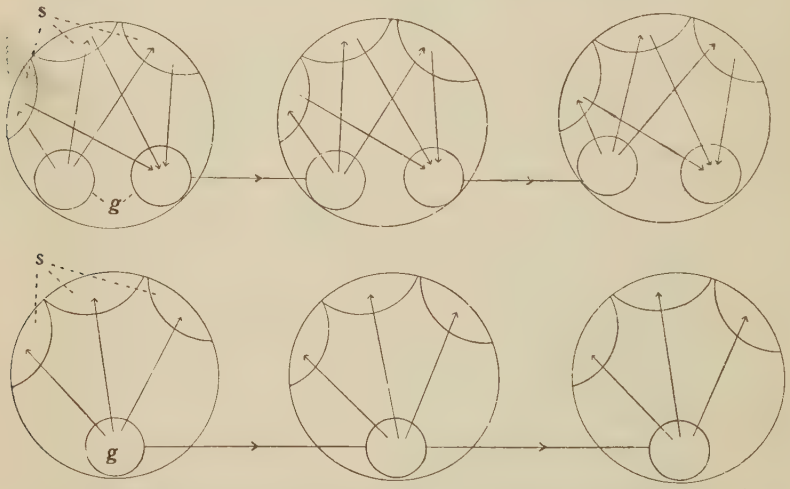

FIG. 176—Schematic representation of theories of heredity. The upper diagrams illustrate Darwin's theory of pangenesis. *s*, various kinds of body cells from which gemmules are given off which collect in the germ cells, *g*. The latter give rise to successive generations and their component body cells as indicated by the arrows. The lower series illustrates Weismann's conception of the continuity of the germ plasm and the derivation of the body cells, *s*, from the germ cells, *g*.

ingenious, though highly speculative, and it has the merit of bringing together many facts of heredity and variation under a common point of view. Nevertheless, it failed to secure many adherents. The fundamental assumptions of the theory are inconsistent with the facts of physiology, and direct evidence for them is entirely lacking. Moreover, much has been learned

in regard to the probable basis of hereditary transmission, and this knowledge has given us a picture of the process very different from the one presented by the theory of pangenesis.

One of the first to question the Lamarckian theory was Francis Galton, but skepticism on the subject did not become general among biologists until after the theory was attacked by Professor August Weismann. In his early essays on heredity, Weismann developed a theory of transmission based on the idea of the continuity of the germ plasm. The germ plasm, or material basis of heredity, is, according to Weismann, distinct from the body plasm, although it may produce the latter in the course of embryonic development. Germ plasm, strictly speaking, is not derived from the body, although it is carried and nourished by the body. Its source is in the germ plasm of preceding generations. Germ plasm is supposed to be handed on from one generation to the next by a continuous series of cell generations. It is the thread that connects successive generations of individuals together, and these individuals resemble one another because they are all developed from a continuous germinal substance. Heredity, in other words, is due to the continuity of the germ plasm.

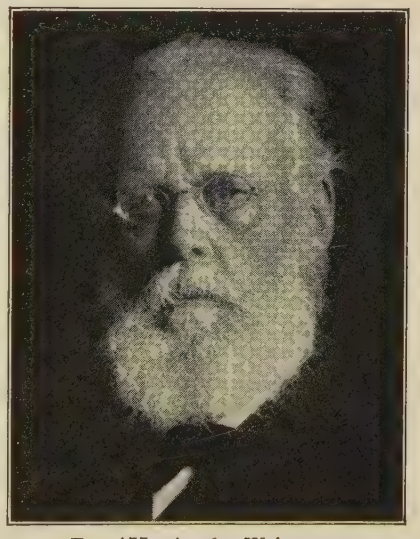

Fig. 177—August Weismann.

This is undoubtedly a very simple and plausible theory. Inasmuch as the germ plasm is derived in every case from antecedent germ cells instead of from the body, it would hardly be expected that characters acquired by the body would be transmitted through the germ cells to the next generation. Accordingly Weismann was led to inquire if there really is sufficient ground for the Lamarckian

theory, and after giving the available evidence a critical examination he concluded that it was quite inadequate.

In the first place, there are many characteristics of organisms to which the Lamarckian theory is, from the nature of the case, inapplicable. Frequently organisms are protectively colored so as to be distinguishable only with difficulty in their natural surroundings. Their colors are not modified by use, since they function in a purely passive way. Consequently the Lamarckian theory cannot explain their evolution. The structural devices of flowers, which enable them to secure cross-fertilization through the visits of insects, present a similar difficulty. Insects in their efforts to obtain honey may cause a certain amount of abrasion or mutilation of the tissues of the flower, but these modifications are not in a direction that better fits the flower for performing its specific function. It is hardly possible to conceive how the parts of a sage blossom, for instance, could have developed their peculiar configuration through the transmission of acquired characters. The same difficulty is encountered in numerous other structural devices of both plants and animals. We must therefore conclude that some other evolutionary factor must be invoked to account for the development of such characteristics. This, of course, does not prove that the Lamarckian factor is not responsible for the development of many structures, but, according to the well recognized logical principle that causes are not to be multiplied beyond necessity, one is justified in the suspicion that other factors may have been responsible for the entire course of evolution without the assistance of the transmission of acquired characters. The arguments for Lamarckism based upon structure are therefore lacking in conclusiveness. The theory is not necessarily true because it gives a plausible explanation of a part of the facts. Whether or not it is true can be determined unequivocally only by the method of experiment.

There have been several experimental investigations of the problem, and the results have been interpreted in different ways. The outcome of experiments on the hereditary effect of mutilations has generally been conceded to be negative even by the

Lamarckians themselves. Several observations have been reported of the accidental mutilation of a parent followed by a corresponding defect in the offspring. Professor Brewer tells of a cock which had lost one eye and which had produced several progeny in which the corresponding eye was missing. A somewhat more striking case is reported by Blumenbach of a man who had his right little finger mutilated and who had a son with a similar defect on the corresponding finger.

These instances suffer from the drawback that they are cases especially selected because they support the theory. There are thousands of mutilations which are not followed by any noticeable effect upon the offspring, and it is evident that many instances might be collected in which parent and offspring happened to have the same defect even if the one defect had no causal relation to the other. Were these curious coincidences really based on a true causal connection, the artificial mutilation of animals should result in the reappearance of similar mutilations in their descendants. In order to test this possibility Weismann cut off the tails of mice for twenty-two successive generations. In not one of the 1592 descendants was a mouse found to be born with a shortened tail. Similar experiments on mice by Cope and Bos yielded the same negative results. For untold generations many savage tribes have subjected themselves to such mutilations as flattening their heads, gashing their cheeks and forehead, boring holes in their lips, and greatly deforming their ears, without producing the slightest disfigurement in their children. These savages certainly had no intention of carrying on experiments in genetics; nevertheless, the fact that their babies are born free from any blemishes indicates that mutilations, even when long continued, have no noticeable influence on the progeny.

Among the experiments designed to test the inherited effect of disuse those of Lutz and Payne on the fruit fly are of especial interest. Lutz kept fruit flies in narrow vials so that they were unable to use their wings in flight. The relative lengths of wing and body were measured in the initial lot of flies and also

in their descendants. The flies were bred in the vials for 43 generations, but at the end of the experiment the relative length of the wings was no less that it was at the beginning. It was formerly customary to attribute the lack of wings in certain kinds of insects to the inherited effects of disuse, but in this case disuse produced no detectable effect.

In order to test the influence of disuse upon the eyes Payne bred fruit flies for sixty-nine generations in the dark, but the eyes of the last generation were as large as those of the first, and in testing the reaction of the flies to light it was found that the functional efficiency of the eyes was apparently unimpaired.

In contrast to the preceding investigations, the results of experiments which have been interpreted as favorable to the Lamarckian theory have generally been obtained in the first generation. In his well known experiments on the transmission of immunity to the poisons ricin and abrin, Erlich accustomed mice to these poisons by very gradually increasing the dosage. Finally, the mice came to tolerate several times the amount of poison that would originally have been fatal. It was observed that the offspring of these mice likewise possessed a high degree of immunity to these same substances. This immunity, however, was transmitted through the female. There was thus an opportunity for the poison in the mother's body to act upon the embryo so that the latter might acquire immunity directly. The immunity was not hereditarily transmitted from one generation to the next; it was acquired by both generations at the same time.

This cannot be considered as a true case of transmission of an acquired character. In order to prove the existence of such transmission, one should produce a specific kind of change through a particular environmental influence on the body, and then ascertain if the offspring, born and raised under normal conditions, exhibit the same kind of specific change. If, for instance, a man were to use his left arm exclusively so that it became much larger and stronger than his right one, and if his offspring should have the left arm considerably better developed

than the right, even though both were given the same amount of use, the fact would afford evidence that acquired characters are transmitted. Let us suppose, however, that an insect is raised with a small amount of food so that it becomes stunted in growth, and that its offspring raised with a normal amount of food is also somewhat stunted. Would this be a case of the transmission of an acquired character? In one sense the lack of growth is acquired. The egg, if smaller than the usual size, would give the larva a relatively poor start in life from which it might never entirely recover. But if we call this a case of transmission of acquired characters, it is a phenomenon quite different from the one previously cited. It is a result which can readily be explained as due to a general change affecting the germ cells in an unfavorable manner.

The transmission of a better developed arm implies that the germ cells are affected in a specific way that enables them to produce the same specific modification in the organism to which they give rise. Our present biological knowledge has revealed no very probable mechanism by which this specific kind of effect can be transmitted to and through the germ cells. And it is significant that most of the experiments cited as favorable to the Lamarckian theory are not cases of such specific transmission. They are mainly interpretable as due to general changes affecting such characters as size, pigmentation, vitality, or an acceleration or retardation of development.

The experiments which seem to afford about the best evidence of the transmission of a specific modification of a particular organ are those reported by Guyer and Smith on the production of hereditary defects in rabbits. These investigators made an extract of the lens of rabbits and injected it into the blood of a fowl. Later some of the fowl's blood was withdrawn and the serum was injected into the veins of pregnant rabbits. It was supposed that the fowl responded to the lens extract by the production of an antibody that attacked the lens substance much as the antitoxin generated in a horse in response to a dose of diphtheria toxin attacks the toxin of that disease. The serum

of the fowl had a very deleterious effect upon the rabbits and some of the young were found to be born with defective eyes. Sometimes the lens was opaque or partially liquefied, and there were

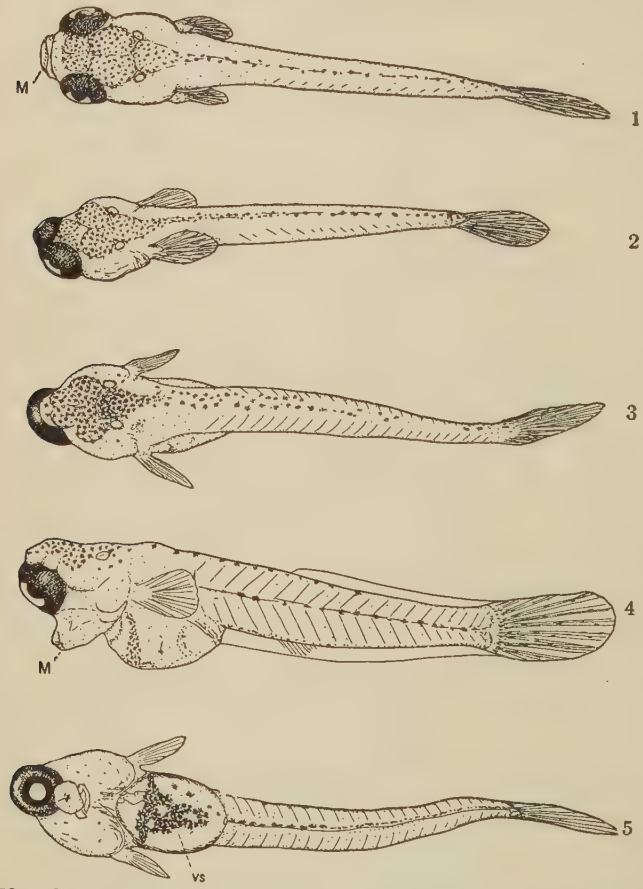

FIG. 178—The effect of solutions of magnesium salts on the development of the fish Fundulus: *1*, normal embryo; *2-5*, embryos raised in sea water to which magnesium salts have been added; *2*, embryo with its two eyes approximated; *3, 4, 5*, three views of an embryo with a single median eye (cyclopia); *M*, mouth; *vs*, yolk sak. (After Stockard.)

also cases of cleft iris and various other defects. The defects of the eye were found to be transmissible as a recessive trait although one of rather irregular and uncertain manifestation.

Some instances were reported of the defect being transmitted through the male sex, a fact that strengthens the assumption that it depends upon a modified Mendelian factor.

It has been suggested that these results are due to the specific influence of a lens antibody upon the genes in the plasm which are especially concerned with the development of the lens. If this were true it would afford something closely analogous to the transmission of an acquired character. In the light of our present knowledge we should be very cautious in interpreting the results of these experiments. Granted that a recessive factor for defective eyes was not carried in the stock and happened to manifest itself a number of times in the experimental animals, the defects might possibly be regarded as a consequence of some change producing a general impairment of developmental energy. But why should this impairment manifest itself as a defect in the eyes? In regard to this matter it should be borne in mind that eye defects are a not infrequent manifestation of a general injury to the embryo. Stockard discovered that embryos of the fish Fundulus raised in sea water to which there were added various salts of magnesium, exhibited defects of the eyes (Fig. 178). In some cases the eyes were found to be fused together so as to produce a single median eye (cyclopia). The same investigator found that eye defects occasionally appeared in some of the descendants of alcoholized guinea pigs. More recently, hereditary eye defects have apparently been produced by Bagg and Little in the progeny of mice subjected to the action of X-rays. These injurious agencies affect development in many ways, but it is noteworthy that eye defects should arise in response to an influence whose action cannot be supposed to be specific. Possibly the lens substance is no more specific in its action than alcohol or X-rays, the eye defects in all these cases being merely one symptom of the action of a deleterious agency.

In the study of the possible transmission of acquired characters there are many opportunities for being misled. A common source of confusion is the failure to recognize the distinction

between a change in the germ plasm arising in response to some environmental agency, and the transmission of an acquired bodily character to the germ cells so that they produce the same character in the next generation. If the alcohol in the body of a drunkard should affect his germ cells so that they give rise to defective children, it is not the character acquired by the parental body that is transmitted, but the modification directly produced in the germ plasm. Dr. Gee has produced defective fish embryos by exposing the free spermatozoa to alcohol and then allowing them to fertilize normal eggs. There is here no possibility of the transmission of a somatogenic character. If sperm cells are affected by alcohol it really makes no difference whether they are acted on within the body, as in the case of the drunkard, or outside of it, as in the case of the fish.

The possible transfer of bodily characters to the germ cells has been tested by grafting ovaries from one breed of animals into another. One may thus ascertain if the transplanted germ cells would give rise to progeny having in some degree the peculiar characters of the animal into which they have been introduced. Castle and Phillips removed the ovaries from a white guinea pig and grafted in their stead the ovaries of a black guinea pig. If bodily characters affected the germ cells the body of the white guinea pig should produce some indication of its influence on the progeny. By breeding the white guinea pig with a white male, progeny were obtained which were all black. There was no evidence that the color of the maternal body had the slightest effect upon the germ cells of the engrafted ovary.

TELEGONY, OR THE INFLUENCE OF A PREVIOUS SIRE

There is, or was until recently, a widespread belief among breeders of animals that the progeny of a given female tend to exhibit some of the characteristics of a previous male parent. If a breeder possessed a valuable strain of pure-bred dogs or horses he was very careful not to allow a female to bear young to a male of inferior quality, lest the qualities of the latter should appear in the progeny subsequently produced by a male of

superior stock. There have been several peculiar cases which seemed to yield support to this old belief, but the theory has not stood the test of critical experimental investigation. Suppose we breed a gray female rabbit heterozygous for albinism with an albino male rabbit. Half of her young might be expected to be albinos. Now suppose the female is bred to a male gray rabbit that is heterozygous for albinism. In her progeny there will probably be one or more albinos, and the breeder who knew nothing of the possibilities of Mendelian segregation might conclude that the albino young were due to the influence of the previous albino male. The observation of such cases as this at a time when the principles of Mendelian inheritance were not known afforded the principal basis for the prevalence of the belief in question.

THE MYTH OF MATERNAL IMPRESSIONS

Another widespread belief, although one with less evidence in its favor, is the old notion that pregnant women who may have experienced a sudden fright or severe mental shock are apt to impress what are commonly called birthmarks upon their children. The belief is a very ancient one, and it is commonly found among primitive people the world over. It has become a part of our folklore, and although it is now universally discarded by biologists and the better trained members of the medical profession, the belief still lingers in the popular mind, and is now and then championed with an air of authority by pseudo-scientific writers of various cults and persuasions. A typical case adduced in its support is as follows: Mrs. A. in a late month of pregnancy put her hand into a bin to get some flour. A mouse happening to run out upon her arm, Mrs. A., like most members of her sex in similar circumstances, was very much frightened. Her child, born soon afterward, had a mark on its arm more or less resembling a mouse. *Post hoc ergo propter hoc*, the birthmark was duly accounted for to the satisfaction of Mrs. A.

The reddish patches on the skin, which occasionally disfigure

people from the time of their birth, have often been attributed to a strong desire of the pregnant mother for a particular kind of food. They have done duty as liver, beefsteak, strawberries, blackberries, cherries, lobster, and no end of other articles of diet, and if their shape was found to bear an imaginable similarity to any object that may have impressed the mother, they have been similarly explained as a result of maternal mental impressions. Of course all the cases of shocks, frights, and strong desires that have left no marks upon subsequently born children are never taken account of. When some anomaly appears in a child a search is made through the history of the mother, and if anything is discovered which can be brought into relation with the event, it satisfies the desire for an explanation. Given a prevalent belief, then the cases which support it naturally accumulate, just as wonders are always happening among credulous people.

THE QUESTION OF NATURE VERSUS NURTURE

There has been a great deal of discussion over the problem of the relative importance of heredity and environment or, as Galton has expressed it, nature and nurture, in the development of organisms. The chief interest has centered in the human aspects of the problem, and here we meet a great diversity of opinions. There are some who hold that the differences among men are mainly due to heredity, while others maintain that they are chiefly the effect of environment. As an illustration of the latter viewpoint we may quote the statement of Mr. Henry George that "the influence of heredity which it is now the fashion to rate so highly, is as nothing compared with the influences which mold the man after he comes into the world." Some have taken the position that the problem is insoluble because we have no common measure by which we can compare hereditary and environmental influences. We are reminded that both heredity and environment are all-important, because without either there could be no organism at all. This is of course true; but we cannot get rid of the problem in this easy

manner; it is continually confronting us in a multitude of forms when we come to grapple with the biological and psychological problems presented by human society. In the abstract, the question is a sterile one. It is heredity that makes the difference between a human being, a fern plant, and a protozoön; it is environment that makes all the difference between a normal living organism, a monstrosity, and no organism at all. But consider the question as it may present itself in a concrete case to the practical farmer who wishes to know whether he can get more eggs by changing his breed of hens or by feeding them on a particular commercial food, instead of the refuse from the kitchen, and the problem becomes one that can be solved by proper experiments in feeding and breeding.

Human beings differ greatly in their inherited physical and mental traits, and they may be profoundly influenced by their environment, but whether heredity or environment is more potent in determining the differences in any given characteristic depends largely upon the particular characteristic selected. Were it eye color, we should have to admit that environment ordinarily has very little effect; the differences between blue, green, or brown eyes are due almost entirely to ancestry. The differences in color between a white man and a negro is certainly a matter of racial inheritance, while the difference in shade between a boy who lives indoors and one who habitually goes bareheaded in the sun may be mainly environmental. The differences in skin color that may be acquired by exposure are not nearly so great as the extremes which are due to heredity. If we limited our inquiry, say to Norwegians, and inquired whether the shades of color among this people are due more to heredity than to differences in exposure, we should have to make a special investigation before we would be justified in venturing an answer. Heredity can make all the difference between an albino and the blackest Ethiopian, and environment can make very great differences in extreme cases. But the problem of heredity versus environment is not what these factors *can* do, but to what extent are the differences commonly

met with in a population due to the differences in the influence of these two causes. This is a problem which it is quite feasible to solve by the proper methods of measurement and comparison. If we wished to ascertain whether heredity or environment is the more potent in producing variations in the skin color of Norwegians we should have to study by means of a color scale, or some other method of measuring color, the extent of color variation that goes along with environmental changes. The student of biometry trained in the methods of statistical investigation would be able to do this, and to express his results quantitatively in a coefficient of correlation. Such a coefficient would express the degree to which the two things tend to vary together. It is indicated by some fraction of unity, the number 1 representing perfect correlation. He could also ascertain the degree in which shades of color in offspring tend to resemble the shades of color in parents, and he could express this also as a coefficient of correlation. Then he would compare these two correlations and find which is the greater. By this means he would get a measure of the relative influence of heredity and environment upon the development of a particular characteristic within a given population. If he carried on a similar investigation with a different population, say in a ward of an American city containing Norwegians, Italians, Negroes, and Chinese, he would get a higher correlation for heredity. In other words, heredity in this case would be *relatively* more influential in producing the different colors met with than among the Norwegians.

The question of heredity versus environment is continually presenting itself in problems of disease. Whether or not we contract the plague, hydrophobia, or smallpox is mainly determined by the accidents of our environment; but there are several diseases, such as diphtheria and scarlet fever, which are not taken by all who are exposed to them, and there is some evidence that this is due to a natural immunity which is transmitted through heredity. In the absence of the inciting environmental factor in the form of specific disease germs these

diseases would not exist. Nevertheless, their actual distribution in a population is dependent upon both hereditary and environmental factors. There is evidence that tuberculosis characterizes certain family stocks much more than others, but this has been explained by some writers as due to the direct transfer of contagion from parents to children, and the fact that both parents and children often live in surroundings that predispose them to contract the disease. On the other hand, many investigators, including Pearson, Goring, Goværts, and Pearl, contend that familial tuberculosis depends upon a hereditary proclivity, or diathesis. Experiments on guinea pigs under environmental conditions which have been rendered constant have shown the existence of hereditary differences in susceptibility to tuberculous infection. Tuberculosis, like germ diseases in general, is contagious, but whether it is contracted or not, and especially whether it runs a mild or a severe course, probably depends to a considerable degree upon the heredity of the stock.

Both heredity and environment are important factors in insanity. The forms of insanity are exceedingly varied and so also are the causes. Unquestionably, several kinds of insanity are due to infections. General paresis, and frequently other types, are caused by syphilis. Many cases of insanity have been occasioned by some focal infection such as diseased tonsils or bad teeth, and the removal of the exciting cause has often been followed by recovery. Other forms of insanity are apparently due to developmental causes dependent almost exclusively upon heredity. In Huntington's chorea we have a clearly defined type of insanity coming on relatively late in life, usually after the patient has married and had children. The onset of the disease is first manifested by irregular, uncontrolled movements of the hand; the gait becomes unsteady, and there are muscular twitchings of the face, and disorders of speech. As these symptoms develop, mental impairment ensues and usually grows steadily worse until the patient is relieved by death. The disease is transmitted as a Mendelian dominant character. Davenport and Muncie have traced 962 cases in America back to six or seven

ancestors including three brothers who migrated to this country during the seventeenth century. The grave dangers that result from the marriage of persons with ancestors afflicted with this fatal malady evidently failed to impress most members of these families. "When Emma T.," according to Davenport and Muncie, "wished to marry Jesse H. whose mother was choreic, her parents opposed the match on account of the heredity of chorea which was even then (1800) recognized. It is said she replied to their arguments that Jesse was not affected, and that she loved him so much that she would marry him if he were, so that she might care for him. She had to care not only for him but also for four choreic children."

The precise mode of transmission of other forms of insanity is at present obscure. In many cases what is transmitted is rather a proclivity to insanity which under favorable conditions may never betray itself by any decided symptoms; but when worry, severe shock, or disease comes along, the individual may fall a victim to his inheritance. Many so-called causes of insanity merely pick out these hereditarily disposed individuals. Some persons are endowed with such a sound hereditary constitution that they stand up under the severest misfortunes, diseases, and trials without exhibiting the least trace of unsoundness of mind.

There are numerous cases of hereditary insanity in which the disease, like Huntington's chorea, comes on even under the best of environmental conditions and in which nothing seems to be able to stay its relentless course. Insanity, however, is not always inevitable because it is hereditary. An insane diathesis may occur in varying degrees. Whether or not it may be overcome depends, in the first place, upon its original potency, and, in the second place, upon environmental factors. There is disagreement among alienists as to the relative importance of heredity and environment in causing insanity, but there should be no disagreement over the fact that both are sufficiently important to be seriously reckoned with.

The aspect of the problem of nature and nurture which has

elicited the most controversy is its relation to intelligence. Are the intellectual differences between men due mainly to their heredity, or to their environment and experience? Certainly there is no kind of nurture by which a very stupid person can be converted into a genius, although accident or disease may convert a genius into a very stupid person. Galton and others have shown that superior mental ability tends to run in families, and it is an undoubted fact that feeble-mindedness also runs in families. With the lower grades of feeble-mindedness little improvement can be made, even with the best methods of education. More can be done for the morons, or the higher grades of the feeble-minded, but they reach the limit of their tether relatively soon. With the same educational advantages, the minds with superior native intelligence rapidly outstrip their fellows. Intelligence increases with age up to a certain period, but to what extent it is possible to develop real intellectual power, as distinguished from acquiring knowledge and specific aptitudes, is still a matter of dispute. Many psychologists hold that education does relatively little to increase the native capacities of the mind, these being determined mainly by heredity. However this may be, there can be little doubt that the hereditary differences in mentality among human beings are very marked. The recognition of these differences is important, as is now coming to be realized, in relation to our educational, economic, and social problems.

An illuminating sidelight upon our problem is furnished by those interesting individuals known as identical twins. Galton called attention to the fact that twins fall into two classes: (1) ordinary, or fraternal twins, whose resemblance to each other is about the same as that of other children of the family; and (2) identical twins, who are usually very much alike, and always of the same sex. Fraternal twins are the product of different fertilized ova, and they are sometimes very different in physical development, intelligence, and disposition. Identical twins are often so similar that even their parents find difficulty in distinguishing them. There is evidence that identical twins arise

from the same fertilized egg. If so, they would have the same heredity, and whatever differences they exhibit would represent purely somatic, or environmentally caused variability.

Since twins usually have a very similar upbringing, a study of identical and fraternal twins affords a means of comparing the effect of similar nurture and like heredity with the effect of similar nurture and unlike heredity. The resemblance of iden-

FIG. 179—Two very similar twin girls, probably identical twins. (After Wiggam.)

tical twins often reveals itself in peculiar and striking ways. Among twins apparently identical, there are many cases of insanity which began at nearly the same time and exhibited much the same symptoms. A remarkable case of resemblance in superior mental ability as well as in physical traits has been reported by Dr. Gesell in a pair of twin girls. The ancestry was of superior quality, as it was stated that "scientific and linguistic ability of a high order and physical energy are some of the traits which are found in the two immediate generations." Both girls were unusually precocious and began to talk and walk at eleven months. When three years old they began French, and in less than a year they were reading English, French, and

Esperanto. "Formal arithmetic was begun at six and in less than a year they were solving mentally problems in fractions and percentage. At the age of nine both were doing Junior High School work. They speak French fluently, and have made progress in Italian and have embarked upon Russian. They are

FIG. 180— Two remarkably similar twins. Over the left eye of each twin there is a small mole. The two men are very much alike in manner and other qualities, and their voices are almost indistinguishable. (After Wiggam.)

much alike in their tastes and dispositions. Their mental tests and their vocabulary tests give almost the same scores."

In their physical measurements the two girls were remarkably alike. They exhibited the same reactions to blood tests and to vaccination. The palm prints and the prints of the soles of the feet were so similar that the same descriptive formula applied to both. At eight years of age the right upper incisor tooth was in the same stage of retarded development, and on the

upper lip of each, a little above the outer corner of the mouth, was a small, pigmented mole.

One of Galton's correspondents writing of a pair of twin boys says: "They have had *exactly the same nurture* from their birth up to the present time; they are both perfectly healthy and strong, yet they are otherwise as dissimilar as two boys could be, physically, mentally, and in their emotional nature."

FIG. 181—Hands of the twins represented in the preceding figure, showing an unusual fold behind the third finger. (After Wiggam.)

When we compare such cases with the remarkable similarities presented by the two girls described by Dr. Gesell, we cannot help being strongly inclined to agree with Galton when he says: "There is no escape from the conclusion that nature prevails enormously over nurture when the differences of nurture do not exceed what is commonly to be found among persons of the same rank of society and in the same country."

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CHAPTER XVI

ORGANIC EVOLUTION

A. HISTORICAL ORIENTATION

The world of life presents an almost infinite variety of different forms. The species of animals that have been described number several hundred thousands, and the total number of living species must certainly be over a million, and may be several millions. When we add to these the numerous species of plants, and reflect that the existing species of plants and animals constitute but a small fraction as compared with the number which have lived in previous geological ages, we may be able to form some conception of the vast multitudes of different forms which have come into being upon our earth. How did all these diverse creatures arise?

Less than a century ago it was the prevalent belief that each species was created much as we find it today. The doctrine of creation applied to species is a manifestation of a general tendency of mankind to attribute to supernatural causes the occurrence of phenomena which cannot be readily explained. Ideas of natural law and the uniformity of nature have but slowly supplanted the conceptions of a primitive cosmogony, the belief in the supernatural origin of species being one of the last to hold out in the light of advancing knowledge.

Although it is only recently that the theory of evolution has come to prevail, we nevertheless find suggestions of it even in ancient times. Theories of the naturalistic origin of living beings were advanced by Democritus, Anaximenes, Heraclitus, Diogenes of Apollonia, Empedocles, and other Greek philosophers, but it is doubtful if any of these speculators had the modern conception of evolution as the derivation of higher from lower forms of life. They believed instead that all kinds of living

beings had an independent natural origin from the materials of the earth. Aristotle, however, who was a naturalist as well as a philosopher, apparently held to the gradual succession of living beings from the very simplest up to man, but it is not certain that he believed that species actually arose from others by a process of descent.

For the first sixteen centuries of the Christian era the doctrine of evolution was practically in abeyance. The teachings of the first chapters of the book of Genesis were held to establish the doctrine of creation beyond question, and any active opposition to the prevalent conviction would have been very unpopular, if not dangerous. During the seventeenth and eighteenth centuries thought gradually became more emancipated from theological dogma. Among speculative philosophers the theory of evolution had been sympathetically discussed by Bacon, Leibnitz, Hume, Spinoza, and especially Kant. Near the middle of the eighteenth century the great French naturalist Buffon (1707–88) expressed a belief in the mutability of species as a result of the influence of climate and other physical surroundings. While he pointed out many of the structural indications of a common origin for the members of different groups of animals, he vacillated between the advocacy of evolution and the expression of a pious adherence to the doctrine of special creation, so that his real opinions have proven a source of much perplexity to subsequent interpreters. Apparently he was very desirous of presenting the facts which favor the doctrine of evolution, but his deference to the teachings of the Church (for he had some unpleasant encounters with ecclesiastical authorities on account of his heretical opinions) led him to profess belief in the accepted doctrine of creation at the same time.

In England, Dr. Erasmus Darwin (1731–1802), the grandfather of Charles Darwin whose name is now so closely linked with the doctrine of evolution, set forth with much force and in considerable detail various evidence that all organisms are descended from a common primitive ancestral form, or, as he expressed it, "from a similar living filament." In Germany,

the poet Goethe (1749–1832) dwelt upon the evidences for evolution in his essay on "The Metamorphoses of Plants" and in his various writings on comparative anatomy. Even in his eighty-first year he followed with keen interest the debates over evolution in the French Academy which were carried on by Cuvier and St. Hilaire. The conception of unity of type which persists throughout a group of organisms appealed strongly to Goethe's imagination, and he explained this unity as due to a common inheritance, the various modifications of the type being the result of adaptations to the conditions of the outer world.

Perhaps the most prominent of the evolutionists before the time of Charles Darwin was the French naturalist Lamarck (1744–1829) whose chief work on evolution, *La Philosophie Zoologique*, is devoted to a presentation of the evidences of descent, and a consideration of the influence of environment and activity in the production of evolutionary changes. Lamarck had little influence upon his contemporaries. Evolutionary speculations were attacked and ridiculed by Cuvier (1769–1832) who was then the dominant figure in the zoölogical world. Nevertheless, evolution was coming to be looked upon with favor by an ever increasing number of naturalists.

Herbert Spencer deserves a prominent place among the pre-Darwinian evolutionists, although most of his works were written after the appearance of Darwin's *Origin of Species*. In 1852, Spencer advocated the theory of evolution in a vigorous and closely reasoned essay entitled "The Development Hypothesis," and in 1855 appeared his highly original *Principles of Psychology*, a distinctive feature of which is the treatment of mind from the evolutionary point of view. Spencer's great life work, the *Synthetic Philosophy*, deals with biology, psychology, sociology, and ethics from the standpoint of the law of evolution which he attempted to deduce, in his introductory volume on *First Principles*, from the general laws of matter and motion. Spencer ranks as, *par excellence*, the philosopher of evolution, and his writings exerted a profound influence upon the thinking of his day and generation.

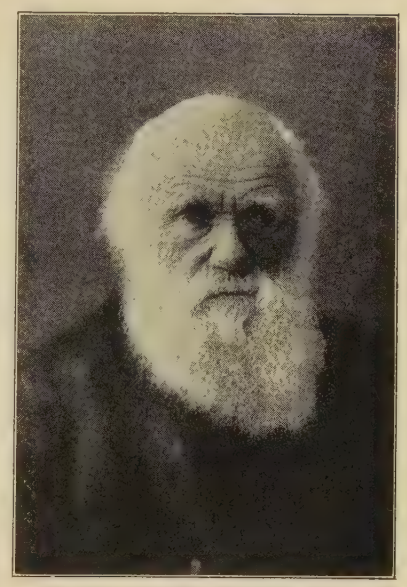

FIG. 182—Charles Darwin.

The most memorable date in the history of the theory of evolution is marked by the appearance of Darwin's *Origin of Species* in 1859. Darwin's great work supported the theory with a great wealth of facts drawn from a variety of fields and marshalled with rare skill and judgment. It also supplied, in the doctrine of natural selection, a good working hypothesis as to how evolution might have been brought about. Few books have aroused such immediate and widespread attention. It was the subject of numerous attacks from pulpit and press, and while it was received favorably by a few eminent biologists such as Huxley, Hooker, and Asa Gray, it met with no little opposition on the part of scientific men. The eminent geologist Sir Charles Lyell, who had hitherto opposed the doctrine of the transmutation of species, soon declared himself an adherent of Darwin's views. In Germany, evolution found a vigorous and able champion in Professor Ernst Haeckel, whose more popular works on *The Natural History of Creation* and *The Evolution of Man* exerted a wide influence in favor of the new doctrine. The years following the publication of *The Origin of Species* constituted a controversial pe-

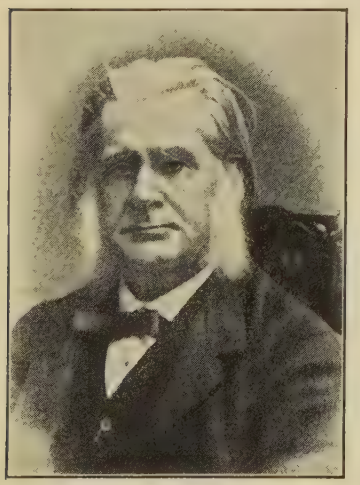

FIG. 183—Thomas H. Huxley.

riod in which a great, new, and revolutionary conception was gradually winning its way to general acceptance in the world of scholars. Scientific men are now practically unanimous in adopting some form of the doctrine of organic evolution. They differ as to the cause of evolution, and they hold all sorts of opinions in regard to Darwin's doctrine of natural selection. But evolution, in some form, has now come to be as much a part of the prevailing scientific conception of nature as the Copernican system of astronomy, or Newton's laws of motion.

That the theory of evolution came to be established as late as the latter half of the nineteenth century may seem at first a strange and anomalous fact. The reasons for the tardy acceptance of the theory are to be found partly in the influence of current theological ideas, and partly in the late development of several branches of science. Not many decades ago life was regarded as having existed on the globe for only a few thousand years. A widely accepted date of creation, which was deduced from the Old Testament narrative, places this event in the year 4004 B.C. It is not surprising that the teachings of geology, which reveal the gradual development of the earth extending throughout many millions of years, met with long and bitter opposition. The science of geology had made but little progress until the latter part of the eighteenth century, and during the first half of the nineteenth century its devotees were denounced for the heretical character of their teachings. Although the nature and significance of fossils had been correctly interpreted by many writers, it was mainly during the first part of the nineteenth century that it came to be generally recognized that previous geological periods were characterized by faunas and floras very unlike those existing today, and that there is a succession of forms of life of gradually advancing organization as we pass from the older to the more recent geological strata. Naturally, so long as it was held that the earth was a creation of only a few thousand years ago, no theory of evolution could gain much headway. Then the subject of comparative morphology, which furnishes so many convincing evidences of descent,

was little studied before the nineteenth century. It is true that much had been learned about the structure of both animals and plants, but it was only when comparative studies were made that a need for a rational interpretation of homologies, unity of type, and the existence of rudimentary organs came to be felt. The science of embryology also made relatively little advance before the nineteenth century, and the cell theory, which figures so prominently in the interpretation of embryonic development, was placed on a firm foundation only in 1838-39.

A sound basis, therefore, was not laid for the theory of evolution until a relatively late period in the history of science. The writings of the earlier evolutionists made little impression upon the thought of their time. Nevertheless in the period immediately preceding the announcement of Darwin's theory, scientific men were growing more and more dissatisfied with the doctrine of special creation, and many were casting about for an interpretation of the origin of living forms which was more satisfying to the scientific understanding. *The Origin of Species* came at an opportune time, and, despite the uproar which it created, its author lived to see the general doctrine of evolution accepted by almost all noteworthy men in the field of biology.

B. GENERAL EVIDENCES FOR EVOLUTION

Evidences for evolution are derived from several sources.

There is, of course, a general presumption in favor of the theory of evolution arising from the fact that our experience with the universe teaches us that things happen in accordance with natural law. We usually believe without question that inorganic objects have come to be what they are through a series of natural events. If we find a rock near the margin of a stream we should not think of appealing to a miracle in order to account for its presence. Were I to come home and find a strange cat in the house I should not think of concluding (nor would the most ardent creationist conclude) that the cat had been created during my absence. So far as our experience goes, cats arise by a process of generation from other cats. Even had I felt perfectly

sure that no cats were in the house when I left, and that they could not have entered from the outside, I should hesitate long—and I think most other people would also—before concluding that the cat in question was the product of a miraculous creation.

Now if I shift my inquiry from the origin of this particular cat to the origin of the kind of cats to which she belongs, what conclusion should be drawn? Direct experience here comes to our aid since it discloses many cases of organisms coming from other organisms of a slightly different kind. Cats differing from other members of their species in possessing six instead of five digits, or in showing distinctive peculiarities of color, have been known to arise occasionally as variations, or mutants. Consequently, in my inquiry, I should naturally look for related varieties or species in the hope of finding one from which our variety might probably have been derived. I might not be able to prove that any one of the numerous species of cats supplied the ancestor sought for, but my search, if sufficiently extended, would reveal many facts of great significance in regard to the probable derivation of cats in general. It would show that, although domesticated cats differ considerably in different countries, they often strikingly resemble the indigenous wild species. And my search would also reveal numerous gradations in the degree of divergence between differences which are barely discernible and those which characterize very distinct types.

One who believes that species were miraculously created would find it very puzzling to decide as to what forms arose from others by the natural process of generation, and what forms were the product of a special creation. He would have to admit that the naturally generated and the miraculously created forms strikingly resemble each other in having much the same catty aspect and much the same catty ways. And he would find himself in a very difficult position if he attempted to show that while natural causes could account for the origin of the cats of the group A, they could not account for the origin of the slightly more divergent cats of the group B.

The thesis defended by Mr. Darwin in his epoch-making

work was that species gradually arose from other species through the accumulation of small variations. Varieties he designated as incipient species, and he thought that just as varieties might in time come to be distinct species, so species might become sufficiently different to be members of different genera. The theory of evolution is simply a consequence of the extension of our ordinary observations on the derivation of organic beings. The origin of organisms by generation from other organisms is the only kind of derivation that we know, and if there ever has been any other kind, the burden of proof naturally falls upon those who maintain that thesis. No one, so far as I know, has ever claimed to have seen a species created. Neither has any one seen a species evolved from other species, but within a relatively few generations man has witnessed the origin of numerous mutations, and he has produced extensive modifications in many kinds of plants and animals. There is no reason to doubt that species, genera, families, and larger subdivisions might have slowly arisen through the accumulation of differences of the kind which have actually been observed to arise. The geologist who observes stratified rocks which total many miles in thickness, and who is familiar with the way in which sedimentary deposits slowly accumulate at the bottom of the sea does not hesitate to regard these rocks as the result of the gradual accumulation of sediment, even though the process must have required millions of years. If an uneducated peasant is asked concerning the origin of the hills, mountains, and valleys of his environment he would probably reply that they have always been much as they now are ever since the beginning. The geologist, on the other hand, sees the story of the earth's evolution written in the rocks. He interprets the great changes of the past in terms of the small changes taking place in the present. His scientific imagination enables him to discern the historic meaning of the present configuration of the earth. He requires no sudden cataclysms or miraculous interventions in order to explain the successive transformations of the earth's crust; he can account for them, in an entirely satisfactory way, as the result of known causes of geological change.

In a somewhat similar manner the biologist pictures organic evolution as brought about by the gradual development of one kind of organism from another through the accumulation of such changes as may be seen to occur at the present time. He thinks of living beings as having slowly evolved through long geological ages from lower to higher types and finally culminating in the development of man. How do the phenomena of organic life fit into the biologist's picture?

C. THE EVIDENCE FROM CLASSIFICATION

Let us consider first the facts of classification, or the way in which organisms fall into groups. Owing to the vast number of different kinds of plants and animals found in various parts of the earth, the task of describing and classifying species has long formed one of the chief occupations of botanists and zoölogists. The great Swedish naturalist Linnæus initiated a number of reforms in preceding schemes of classification, one of these reforms being the system of binomial nomenclature, in accordance with which each species is given two names, one designating the genus, the other the species. Thus in *Ursus americanus*, the name of the common black bear of North America, *Ursus* represents the genus, and *americanus* the species. A genus includes a number of related species. In the genus Ursus, for instance, there is also *Ursus horribilis*, the grizzly bear, *Ursus arctos*, the European brown bear, and many other species in different parts of the world. Linnæus recognized that a species might give rise to varieties, but he held that these cannot diverge indefinitely, as they are confined by their nature within certain prescribed limits of variability. "We reckon," he says, "as many species as issued in pairs from the hands of the Creator." In agreement with the English naturalist, John Ray, Linnæus came to hold that species differ from varieties in being infertile when crossed, or in producing progeny which, like the mule, are sterile, so that each species is enabled to retain its distinctive characteristics with no more than a very limited amount of variation. This conception of species became the dominant

one among systematic botanists and zoölogists up to the time of Darwin.

Linnæus essayed the task of describing and classifying all the known species of plants and animals in his great work entitled the *Systema Naturæ*. The *Systema Naturæ* ran through twelve editions in the lifetime of its author, and, although the work naturally grew bigger with each edition, it was still possible in the latest issue to include brief descriptions of all known species of plants and animals within the limits of a single work. Linnæus clearly perceived that the classification of species should not be carried on in an arbitrary way, although he employed an artificial system in the grouping of plants. There is, he contends, a "natural," or true sytem of classification which it is the function of naturalists to discover and embody in their systems. We may arrange books in a library according to several artificial methods, such as the nature of the contents, the names of the authors, the color of the bindings, or in any other way suitable for the purpose in hand, but living beings fall into natural groups of their own accord. The various kinds of cats previously mentioned really belong together, regardless of whether they are large or small, or gray, black, or yellow. The species closely allied to our domestic cats are placed in the genus *Felis*, a group which contains the lion, the tiger, the puma, the leopard, and a considerable number of other species in several countries of the globe. The genus *Felis*, together with the allied genus *Lynx* and some others, constitute the Felidæ, or cat family, which is characterized by possessing many common features of structure and behavior. Any one would easily recognize these animals as really belonging together in any rational system of classification. According to the same general method of grouping, the Felidæ, the Canidæ (which includes the dogs, wolves, jackals, and their relatives), the Ursidæ (or bear family), the Viverridæ (or civet family), etc., are placed together in the order Carnivora, or flesh-eaters, a group characterized by a general similarity of dentition and many other common features of organization.

Various other orders, such as the Rodentia (rats, mice, rabbits, etc)., the Ungulata (horses, deer, cattle, etc.), the Chiroptera, or bats, constitute the class of Mammalia, the members of which possess many structural peculiarities in common, chief among which are the mammary glands for supplying the young with milk. Corresponding to the class of mammals there are other groups of animals—the birds, reptiles, amphibians, and fishes—which agree in possessing a vertebral column, dorsal nerve cord, red blood, and several other fundamental features of structural organization by virtue of which they are all included within the large group known as the Vertebrata. And this extensive group, or subphylum, along with the tunicates, Amphioxus, and a few other primitive forms that possess a dorsal nerve cord and a notochord in some period of their life, constitute the phylum Chordata.

The Chordata represent one of the basic subdivisions of the animal kingdom, but coördinate with this great group there are the Mollusca, Echinodermata (starfish, sea urchins, etc.), Cœlenterata (hydroids, jellyfish, coral polyps), Arthropoda (insects, crustaceans, spiders, etc.), and several other phyla each of which exhibits a distinct fundamental plan of structure. If we pass to the plant world we find a similar grouping of forms into corresponding categories of classification.

The arrangement of organisms into groups within groups leads to a system of classification which has often been compared to the branching of a tree. The larger branches correspond to the phyla; the smaller ones to the classes, orders, and families; and the terminal twigs to the species. Some of the older naturalists endeavored to arrange organisms in a linear series, but it is quite evident that species cannot be made to fit into such a system. That they fall naturally into the treelike system of grouping is very readily explained if we assume that they are the product of gradual divergence along with descent from a common ancestor. The general features that characterize the members of any group would then be explained as due to a common inheritance from some ancestral species. As Darwin remarks,

Expressions such as that famous one by Linnæus which we often meet with in a more or less concealed form, namely, that the characters do not make the genus, but that the genus gives the characters, seem to imply that some deeper bond is included in our classifications than mere resemblance. I believe that this is the case, and that community of descent—the one known cause of close similarity in organic beings—is the bond, which, though obscured by various degrees of modification, is partially revealed to us by our classifications.

When we observe people living in the same region who look very much alike we commonly infer that they are related, *i. e.*, we appeal to community of descent as an explanation of their resemblance. Likewise we assume that the resemblances within the racial stock to which they belong are due to the same cause. No one supposes that the Scandinavians, French, Italians, and Greeks, are the descendants of separately created ancestors. All of these people belong to the Caucasian race, and their similarities are always attributed to a common, though remote, ancestry. The human race in general falls into the same system of groups within groups that is exhibited by the subdivisions of plants and animals. Likewise the languages spoken by different peoples and races fall into the same type of arrangement. From the different dialects of the same country there are all degrees of difference in speech up to such distinct languages as Latin and Chinese. In many cases, as may be illustrated by the Romance languages (French, Italian, Spanish, and Portuguese), it is a matter of history that the divergent tongues arose by a process of evolution, and linguists are now in general agreement that all languages developed in the same way.

Naturalists have often commented on the fact that different characters have very different values for purposes of classification. If we classify organisms according to an arbitrarily chosen character, we may group together forms which differ profoundly in all other respects except in possessing the character selected. Were we to put into one group all of the legless vertebrates, we should include such creatures as lampreys, eels (which are limbless fish), snakes, and certain legless lizards and amphib-

ians—a heterogeneous assemblage of animals really belonging to several different classes. If, on the other hand, we based our grouping on the possession of hair we should include nothing but the members of the class of mammals. The value of a character for classification depends upon the extent to which it is an index of the presence of other features of organization. If an animal has true hair it will also have mammary glands, a four-chambered heart and warm blood. If it is simply devoid of legs, we cannot safely predicate what other characters it may have, as it may be a snake, an eel, or even an angleworm.

It has long been recognized also that the value of a character for classification is not determined by its functional importance; in fact, as De Candolle has remarked, it often stands in inverse relation to its functional importance. Rudimentary organs are considered especially valuable as indications of affinity. The presence of rudimentary limbs in certain snakes is a good evidence of affinity with animals bearing limbs, since the only rational interpretation of these rudiments is afforded by the theory that snakes descended from ancestors in which these appendages were functional.

The grouping of organisms in the natural system of classification is one which would be inevitably brought about by descent with modification, as is exemplified in the origin of races, varieties, languages, and other admitted products of evolutionary changes. Only an arbitrary line can be drawn between varieties and species. Varieties are related to species as species are to genera, genera to families, families to orders, and so on. Linnæus, later in life, came to hold that the species of a genus descended from a common created form, but if we assume a common descent for the species of a genus, we can with as much reason make the same assumption for the genera of a family, or the families of an order. The position of Linnæus is much like that of a geologist who would admit that the natural processes of sedimentation might produce strata ten feet thick, but that they could not produce strata a hundred feet thick.

D. THE EVIDENCE FROM MORPHOLOGY

The argument for evolution based on morphology, or the science of structure, has much in common with the argument from classification. It is based upon the resemblance of organisms in structure and the ability of the theory of evolution to explain these resemblances as due simply to inheritance from a common ancestor. As we have already seen, the members of any natural group possess a common plan of organization which is retained, no matter how great the changes which have occurred in adaptation to diverse conditions of life. In the great class of insects, for instance, the most extensive group in the animal kingdom, this fundamental plan is always clearly manifest. The same number of segments is apparently retained throughout the group. Herbert Spencer, in commenting on this circumstance, pertinently asks:

> Why under the down-covered body of a moth and under the hard wing-cases of a beetle, should there be discovered the same number of divisions? Why should there be no more somites in the Stick-insect, or the Phasmid a foot long, than there are in a small creature like the louse? Why should the inert *Aphis* and the swift flying Emperor-butterfly be constructed on the same fundamental plan? It cannot be by *chance* that there exist equal numbers of segments in all these multitudes of species. There is no reason to think it was *necessary*, in the sense that no other number would have made a possible organism. And to say that it is the result of *design*—to say that the Creator followed this pattern throughout, merely for the purpose of maintaining the pattern—is to ascribe an absurd motive.

The same principle of unity of plan is beautifully exemplified in the Crustacea. Consider such a creature as the crayfish or the lobster. The body, as in the other members of the order Decapoda to which these forms belong, is composed of twenty segments. Most of these segments bear each a pair of appendages whose plan of structure is the same, although the appendages are modified to serve the very diverse functions of smell, touch, mastication, prehension, walking, carrying eggs, and swimming. In studying

these organs one seems almost compelled to think of them as resulting from the transformation of a series of originally similar appendages. This interpretation is amply confirmed when we compare them with corresponding organs of the more primitive crustaceans. In the latter, certain organs which in the lobster are used for mastication are employed for ordinary locomotion. Among the crustaceans we find that where more organs are used for locomotion fewer are used for mastication, and vice versa. There seems to be no good physiological, or teleological reason why crustaceans with a large number of locomotor appendages require a less number for chewing their food, but this relation, like many others, is intelligible if we assume that these forms are descended from a common ancestral type. In all of the crustaceans, the jaws and accessory jaws (mandibles and maxillæ) are homologous with legs, and it is of interest to observe that in that living fossil, the horseshoe crab (which has very little in common, by the way, with the true crabs), there are no special organs of mastication, this function being performed by the basal joints of the ordinary walking appendages.

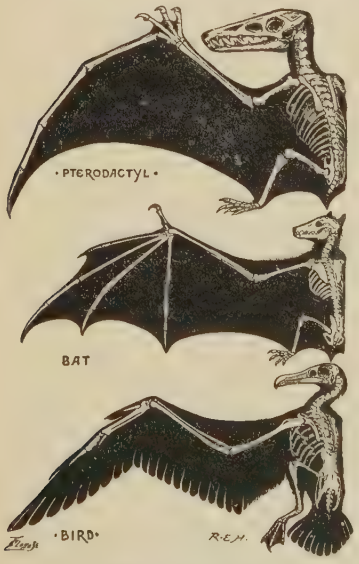

FIG. 184—Different modifications of the fore limb in adaptation to the function of flight. (After Romanes.)

A striking instance of the diverse modifications of organs having a common plan of structure is afforded by the limbs of vertebrate animals. In the vertebrates above the fishes the limbs may readily be conceived as modifications of a common pentadactyl type. In the wing of a bat we find four of the digits enormously elongated to form supports for the web of the wing, the first digit remaining relatively unmodified. In the extinct

pterodactyls only the outer, or fifth, digit is elongated, the three others being of the ordinary prehensile type. In the wing of the bird only three digits are represented, although a fourth is discernible in the embryo. The flying organs in these very distantly related groups are formed on the same fundamental plan as the fore limb of a cat or the arm of a man. They are all readily explicable as having arisen from the modification of a generalized type of pentadactyl limb, the parts of which have been employed in different ways to adapt the organ for the function of flight. We have in these cases an excellent illustration of a very common procedure which is followed by Nature in forming new organs. New functions are usually provided for by the transformation of old structures. The sucking mouth parts of insects are not organs *sui generis*, but they represent transformations of mouth parts of the mandibulate type fitted primarily for chewing. And the chewing mouth parts of insects are homologous with locomotor appendages, as they are in the Crustacea.

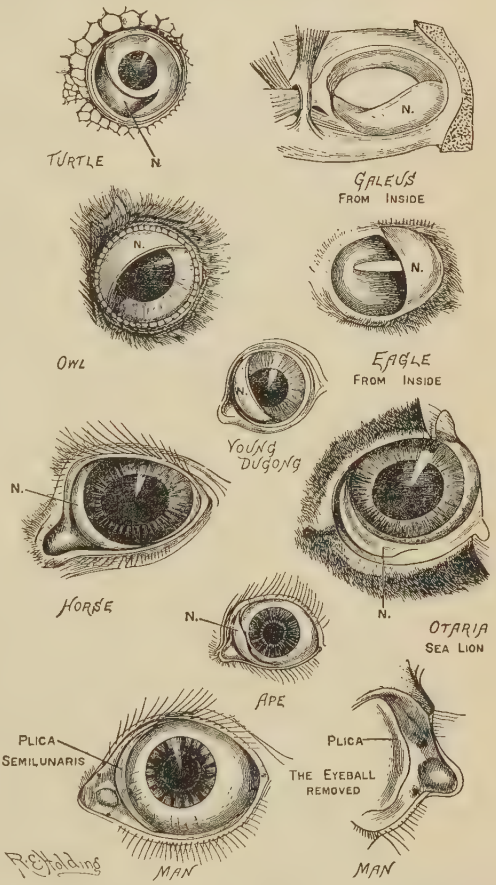

FIG. 185—Nictitating membrane (third eyelid) *N*, in the eyes of vertebrate animals. (After Romanes.)

There are probably no more striking evidences of descent than the rudimentary organs which abound in the structure of most higher animals. We have previously remarked upon the many species with rudimentary eyes, which live in caves. In the inner corner of our own eye there is a small fold, the semilunar fold, which is homologous with the third eyelid, or nictitating membrane of birds and reptiles (Fig. 185). If you watch for a time the eye of a domestic fowl you may observe a semi-transparent membrane which is drawn at intervals across the eye from the inner angle. This third eyelid is functional in most of the birds and reptiles, but it is rudimentary in nearly all the higher mammals as it is in ourselves. We have already mentioned the curious third eye which persists as a rudiment in several species

FIG. 186—Rudimentary muscles of the human ear. (After Gray.)

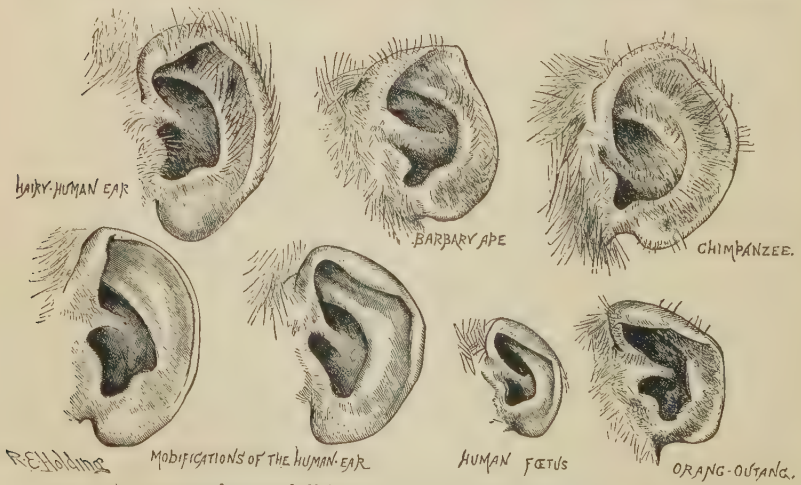

FIG. 187—External ears of different species of primates. (After Romanes.)

of reptiles and amphibians; and its basal portion, the pineal gland, is found in practically all vertebrates. The interesting New Zealand reptile, Sphenodon, which is the only surviving representative of an otherwise extinct reptilian order, has an exceptionally well developed pineal eye with a retina, lens, and nerve, although it is so deeply buried beneath the skin that it is probably no longer functional. The larger aperture on the upper part of the skull of several extinct reptiles suggests that the pineal eye may have been more highly developed in these forms.

FIG. 188—Direction of the slope of hairs on arms and hands of man and the chimpanzee. (After Romanes.)

Our external ear, while perhaps not altogether useless, is considerably reduced in both size and functional efficiency, and it is nearly as much reduced in the higher apes as it is in man. There are three muscles which extend from the cartilage of the ear to the bones of the skull, but in most individuals they are practically functionless. In addition to these, there are smaller muscles confined to the cartilage of the ear which appear to be quite functionless (Fig. 186). If you inspect the ears of your fellow creatures you will observe in a large percentage of cases a small point, now known as Darwin's tubercle, which is situated on the outer rim near the upper side. This represents the

tip of the ear of lower mammals. In many of the apes it is also absent or very inconspicuous, but it is well developed in the more primitive monkeys.

Man is rather exceptional among mammals on account of the

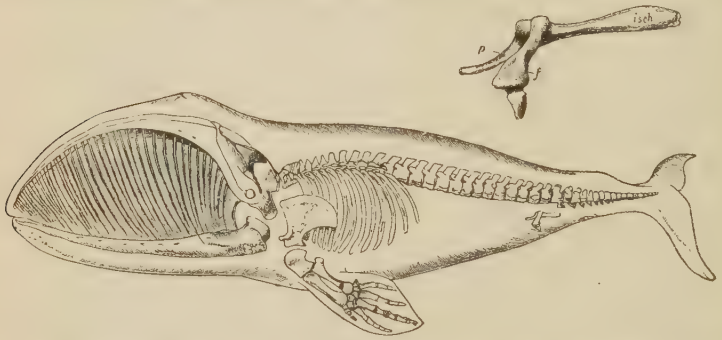

FIG. 189—Skeleton of the whalebone whale. The upper figure represents the rudimentary pelvis (*p*, *isch*) and femur, *f*. (After Romanes.)

scanty development of hair on the body. This characteristic is a very variable one both in individuals and in races. There are very short, fine hairs over a large part of the body, and it

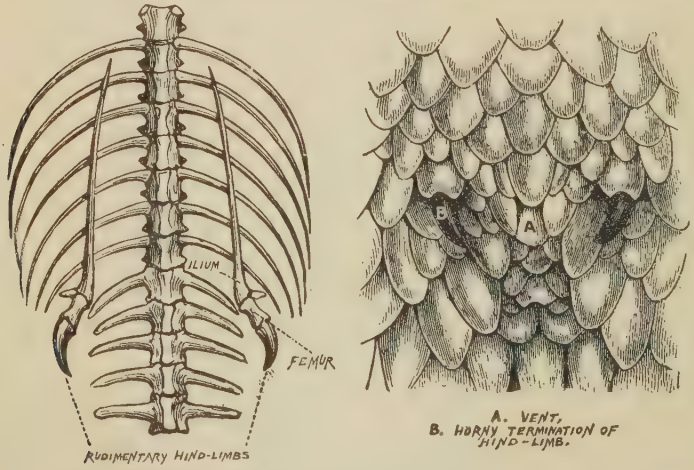

FIG. 190—Rudimentary pelvis and hind limbs of a python. (After Romanes.)

is an interesting fact that the arrangement of these hairs is very similar in man and in the anthropoid apes. In the human embryo

of about the fifth month the whole face and body are covered with a short, fine, woolly hair, the so-called lanugo. This coat normally disappears before birth, but occasionally anomalous individuals occur in which this embryonic hair continues to grow, forming in the adult a long, fleecy covering of the face and body. This character is hereditary and is correlated with deficient teeth.

Besides the rudiments usually present in the human body, there are many other structures occasionally present which are homologous with structures normally found in the lower animals. The gluteus quartus, levator claviculæ, and several other muscles that only occasionally occur in man are regularly present in the apes. The supra-condyloid foramen, an aperture through the outer end of the humerus in several of the monkeys and other mammals, is found in only about one per cent of human subjects. Professor Wiedersheim in his book *The Structure of Man: An Index of His Past History*, has described more than one hundred atavistic structures and peculiarities which occur constantly or occasionally in various parts of our body. Haeckel has designated these structures as "useless primitive heirlooms," but some of them, the vermiform appendix, for example, are occasionally worse than useless.

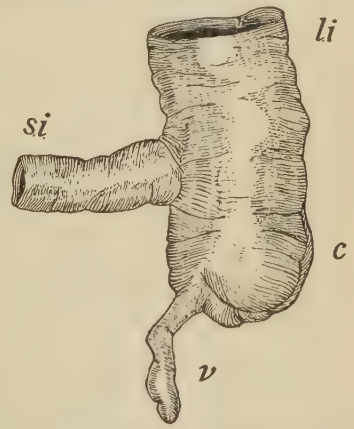

FIG. 191—Cæcum, *c*, and vermiform appendix, *v*, of man; *li*, large intestine; *si*, small intestine.

Some very remarkable structural peculiarities of especial significance in relation to the theory of descent are furnished by a family of crabs, the Lithodidæ, which are unusually abundant on the Pacific Coast of North America. In these crabs the abdomen is more or less asymmetrical, especially in the females, which have appendages for holding the eggs only on the left side. Correlated with the asymmetry of the abdomen there

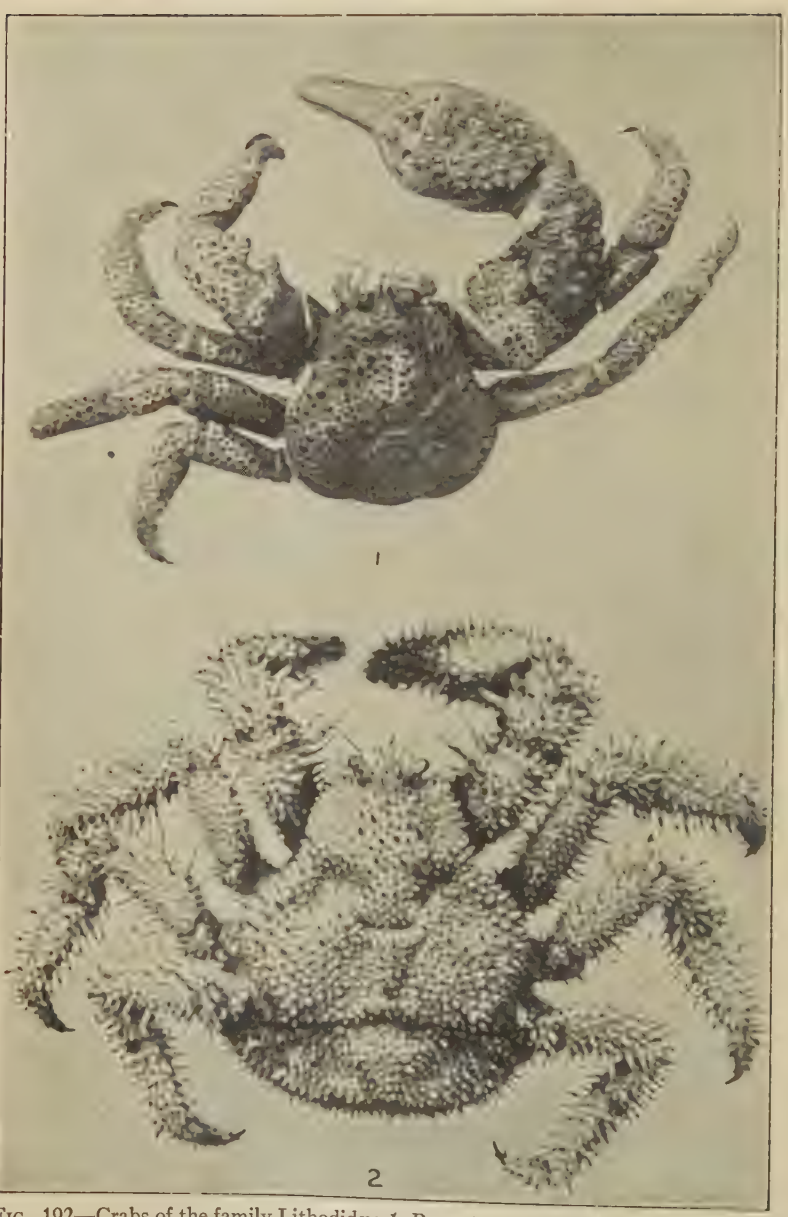

FIG. 192—Crabs of the family Lithodidæ: *1, Dermaturus mandtii; 2, Acantholithodes hispidus.* Note that the right pincer in both is the larger. (After Schmitt.)

is an inequality in the size of the pincers, the right one being uniformly larger than the left. The species of this curious family are exceedingly diverse in form, size, and habits, and there is nothing in their mode of life which suggests any possible utility of their asymmetrical structure. In fact, their abdominal

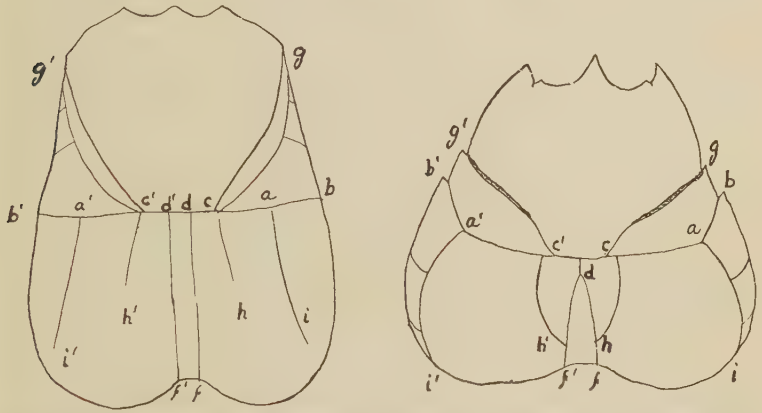

FIG. 193—Upper side of the carapace of a hermit crab Pagurus (left), and *Hapalogaster cavicauda*, one of the Lithodidæ (right). The small letters indicate homologous lines.

asymmetry, and especially the absence of appendages on one side, would seem to be a distinct handicap.

The key to the puzzle is revealed when we study the structure of the nearest relatives of the Lithodidæ, the hermit crabs. Most species of hermit crabs live in the empty coiled shells of gastropod molluscs. The right pincer in the hermits is commonly larger than the left. The abdomen is soft, since it is adequately protected by the shell into which it is inserted. It also shows an asymmetrical twist in adaptation to the coil of the shell, and in most hermits *it has appendages only on the left side.* Since the Lithodidæ are more closely related to the hermit crabs

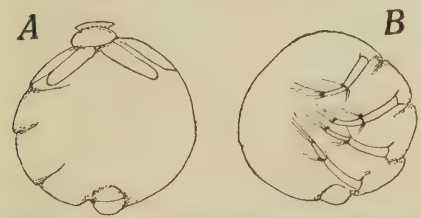

FIG. 194—Abdomen of the female of *Dermaturus mandtii: A*, from above; *B*, from below, showing appendages only on the left side.

than to any other group of crustaceans, the natural inference is that they have descended from the hermits. But while they have taken on a crablike form and mode of life, the loss of symmetry and appendages due to life in the coiled shells of gastropods could never be regained. Teleological explanations of the peculiarities in question are inapplicable; the only rational interpretation is furnished by the theory of descent.

In addition to structural resemblances we may note here another index of genetic relationship which is furnished by blood

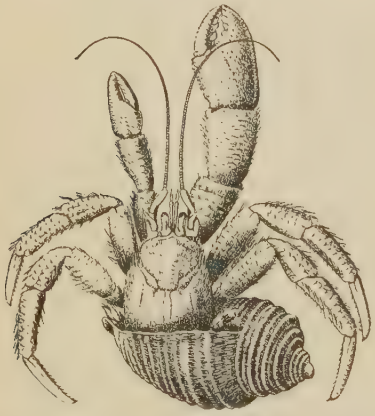

FIG. 195—A hermit crab in a coiled shell. (After Schmitt.)

FIG. 196—A female hermit crab, Pagurus, outside its shell and showing appendages only on the left side of its twisted abdomen. (After Schmitt.)

tests. The blood of animals responds to the introduction of foreign proteins, such as are contained in the blood serum of an alien species, by the production of antibodies. If we make a number of injections of human blood serum into the veins of a rabbit at intervals of one or two days, and then withdraw some of the rabbit's blood and obtain the clear serum, it will be found that the rabbit's serum can be employed as a delicate test for the presence of human blood. When a small bit of human blood is added to the sensitized rabbit serum, it produces a white precipitate. If blood from another kind of animal is introduced, no precipitate, or only a very slight one, is formed. The rabbit's blood has been modified so as to react to human proteins, and

the test of human blood thus afforded is one which has frequently proven of value in the detection of crime.

It has been shown by the extensive and valuable researches of Nuttall and Graham Smith that these blood reactions may

Fig. 197—Photograph of a chimpanzee intent on threading a needle. (After Gregory.)

be used as a test of genetic relationship. While sensitized serum reacts most strongly to the blood of the animal used in producing the sensitized condition, it also reacts more or less to the blood of related species. Even very slight and slow reactions are given to the blood of more distantly related groups, the degree of reaction being roughly proportional to the degree of structural similarity. Blood tests, therefore, afford a means of indicating

affinities. Human blood reacts more strongly with the blood of the anthropoid apes than with that of the other Old World monkeys, and more strongly with the blood of the latter than with that of the New World monkeys, and least of all with the blood of the lemurs. These blood tests are indications of chemical similarity, and chemical similarity parallels structural similarity. Organisms are probably similar in structure *because* they are similar in chemical composition. Blood relationship is not merely a metaphorical expression; it represents a chemical fact, and one which affords important additional evidence of the common descent of the members of related groups.

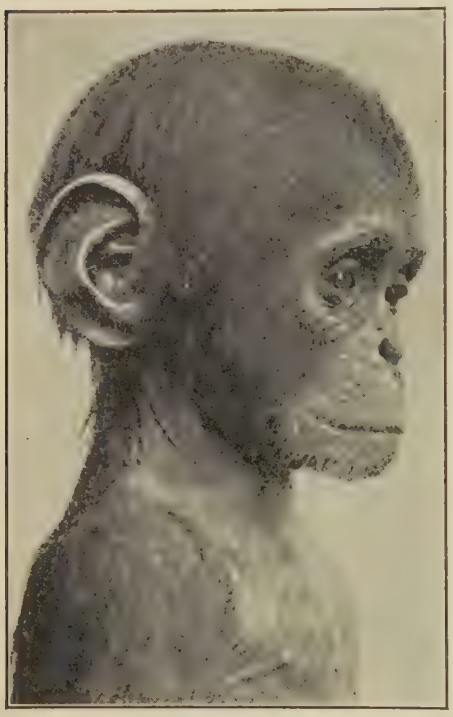

FIG. 198—A young chimpanzee. (From a photograph by Prof. W. T. Shepherd.)

E. THE EVIDENCE FROM EMBRYOLOGY

Organisms resemble each other in the way in which they develop as they resemble each other in their adult structure. It frequently happens that embryos reveal similarities not exhibited by the fully developed organisms. Karl Ernst von Baer, one of the great pioneers in the study of embryology, laid down the principle, since known as von Baer's law, that embryos of different organisms of the same phylum most closely resemble one another in their earliest stages and that the more nearly alike the organisms are, the longer they follow the same path in their development. A mammal and a fish, for instance,

pursue a common course only for a short way, but two kinds of mammals have a closely similar development for a much longer period; and if they belong to allied species they begin to diverge only at a relatively late stage.

In the hands of several evolutionists, the conclusions of von Baer have been employed in the support of a related generalization known as the doctrine of recapitulation, or the biogenetic law. This doctrine, as expressed by Professor Ernst Haeckel, its most prominent exponent, is that "the rapid and brief development of the individual (ontogeny) is a condensed synopsis of the long and slow history of the stem (phylogeny)." Admittedly the resemblances between the two types of development cannot be exact, but, however we may interpret the facts, there is a similarity between the series of forms met with in going from the simplest to the more highly developed animals, and the series of stages passed through in the development of the embryo. Some writers have contended that the embryos of higher animals resemble, not the adults of forms lower in the scale, but rather the embryos of these forms. So far as the evidence for evolution is concerned, this is not an essential point, the important fact being that the embryonic development of different organisms presents points of resemblance that can be rationally accounted for only by the hypothesis of a common descent. Let us note some of these similarities.

In the development of all vertebrate animals there appear on the sides of the neck region a series of slits which in the fishes and many larval amphibians break through into corresponding slits which push out from the walls of the pharynx. Openings are thus created through which water, taken into the mouth, may pass to the outside as it does in the respiration of these animals. Although the gill slits begin in the embryos of reptiles, birds, and mammals, much as they do in the fishes, their further development is soon checked, and as a rule they do not form an open communication with the throat. One of these slits is modified in the higher vertebrates to form the Eustachian tube which leads from the pharynx to the middle ear. Parts of the epithelial

lining of the gill slits develop into the thymus and some other small glandular bodies of uncertain function. But, for the most part, all traces of gill slits disappear in the adult animal.

The gill apparatus in the fishes is supported by a series of cartilaginous or bony arches lying between the slits. The hyoid arch, which supports the tongue, is the homologue of the gill

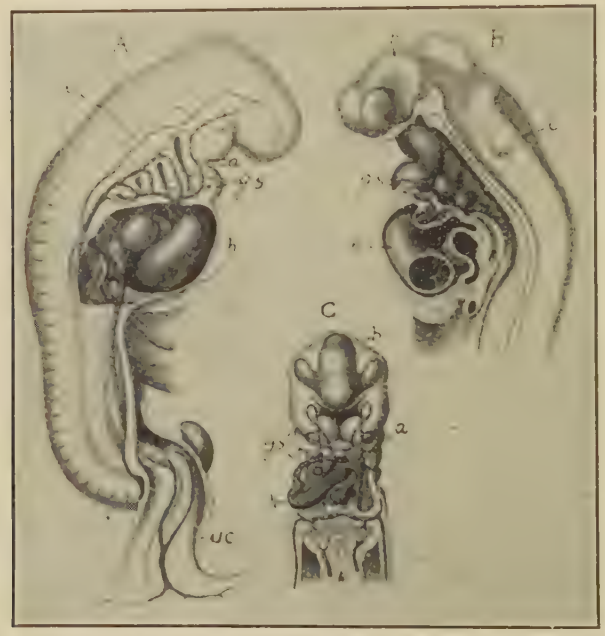

FIG. 199.—Human embryos: *A*, right side; *B*, longitudinal section through the middle; *C*, front view; *a*, arches of the aorta; *b*, brain; *e*, ear vesicle; *gs*, gill slits; *h*, heart; *uc*, umbilical cord by which the embryo is attached to the uterus of the mother. (After His.)

arches lying behind it, but it does not bear gill filaments except in some of the more primitive cartilaginous fishes. In the mammals the hyoid arch is no longer a complete bony structure. Its lower end persists as a part of the hyoid bone; the upper end in many mammals (including man) forms the bony styloid process which fuses with the base of the skull, while the stylo-hyoid ligament, which connects the two parts, makes the hyoid arch complete. In the birds and mammals there is little left of the

gill arches except the ventral ends of two or three of them which are transformed into the cartilages of the larynx.

Corresponding to the gill arches of fishes, there are several arterial arches which supply the gill filaments with blood. The utility of a series of such arches in the fishes is evident, since it allows the blood to be exposed to a larger amount of surface in the filaments of the several sets of gills. But why should we find essentially the same arrangement in the embryos of air-breathing vertebrates? It is a very remarkable fact that

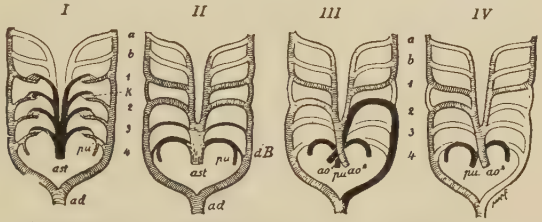

FIG. 200—Aortic arches in different classes of vertebrates: *I*, fish; *II*, a tailed amphibian; *III*, a lizard; *IV*, a bird. Vessels carrying impure blood shown in black; those carrying oxygenated blood shaded; those represented in mere outline are formed in the embryo but disappear in the adult. *ad*, dorsal aorta; *ao*, *ao*², permanent arch of the aorta; *ast*, ventral aorta coming from the heart; *a*, *b*, first two temporary arches; *dB*, ductus Botalli; *k*, gill capillaries; *pu*, pulmonary artery. In *I*, representing one of the lung fishes, *pu* supplies the so-called lung. (After Hertwig.)

in the embryonic development of reptiles, birds, and mammals there are five complete aortic arches laid down very much as in the embryos of fishes, although no gills ever make their appearance. The arterial system, even of a human being, develops as if it were planned to supply blood to the gills of a fish. Afterward, the system is largely broken down, leaving parts only to form some of the permanent arterial vessels of the adult. In the mammals the left half of the fourth arch becomes the arch of the aorta. Parts of the anterior arches are utilized in the formation of the carotid arteries, but the rest of these arches disappear. The pulmonary arteries supplying the lungs are given off from the right half of the fifth pair, only the basal part of which persists. In the birds, which start out with much the same fishlike plan of aortic arches, it is the right half of the fourth arch which persists to form the permanent arch of the aorta.

The arterial systems of amphibians and reptiles present many transitional stages between the arterial system of fishes and that of birds and mammals. The lizard Lacerta, for instance, has two complete and symmetrical aortic arches, although it probably does not need them. Birds and mammals get along with half an arch, and the only reason why the lizard has so many is doubtless because it came from fishlike ancestors. The lizard Lacerta inherits two complete arches in the adult state just as we inherit five of them in our embryonic state.

It not infrequently happens that structures which, according to the theory of evolution, have long been lost, make a temporary appearance in the development of the embryo. Attention has already been called to the rudimentary teeth of fœtal whales and calves. Whales are mainly devoid of hair, there being in some species only a few bristles remaining along the sides of the jaws, but there is sometimes a larger number of bristles that appear in early stages of development. The collar bone is absent in sheep, deer, and many other ruminants, but in the embryo sheep it is completely formed. The jaws of rodents show a space devoid of teeth between the incisors and the molars. Have the teeth in this region been lost? Here again, embryology throws light on the problem, since it has been found in some rodents that several of the missing teeth start to develop, but are resorbed before birth.

These and many other similar facts are quite unintelligible according to the theory of special creation. But they are just what we should expect according to the theory of evolution. Embryos are frequently very conservative in their habits. It takes them a very long time to get over doing things in the same old way after the need for so doing no longer exists.

F. THE EVIDENCE FROM PALEONTOLOGY

If the present inhabitants of the globe are the product of a long process of evolution we should expect to find some indications of the fact in the succession of fossil forms of life. The studies of the geologists have proven that the earth itself has

undergone a long evolution extending through many millions of years. At a relatively early period the surface of the earth became largely or wholly covered with water. As a result of upheavals of the surface, continents were raised out of the primitive shallow seas, and at various periods the crust was thrown into folds that gave rise to chains of mountains. With the elevation of land there began the processes of erosion and deposition of sediments in the bottom of the seas. In this manner stratified rocks were gradually built up whose total thickness has been estimated to be from fifty to one hundred miles. Upheavals occurring at different periods of the earth's history have exposed to view many of the rocky strata deposited in different geological eras. By studying the relations of strata in different regions geologists have been able to piece together a fairly well connected history of the earth's crust. They can determine what deposits are very old and what are relatively recent, and to what particular chapter in the world's history a given series of strata belongs.

It is in the rocky strata that we find the records of the history of life. As Agassiz has remarked, "The crust of our earth is a great cemetery where the rocks are the tombstones on which the buried dead have written their own epitaphs." Records of the existence of living beings have been left in various ways. Sometimes the bones or even other tissues may be preserved as such. Frequently fossil remains are known only from casts. An organism may become imbedded in mud or clay; after its tissues have decayed, the space it occupied becomes filled by the infiltration of foreign material, thereby forming a cast which takes the outline of the organism it replaces. Many forms simply leave imprints due to their settling down upon soft mud. Some of the rare traces of extinct jellyfish are preserved in this way in one of the very oldest fossil-bearing rocks. Sometimes the only records left by certain animals are the tracks which they made on the mud of some ancient shore. A great many organic remains consist of petrifactions. In these, the substances of the organic body are replaced by mineral matter which preserves a faithful

record not merely of external form, but often also of internal structure.

What do these various kinds of fossils teach us as to the evolution of life? The theory of evolution would naturally lead one to expect that the oldest rocks would contain the simplest organisms, and that there would be a gradual advance in the organization of fossil forms as we pass to more recent periods. Were we to find that the most highly developed creatures were in the oldest deposits, and that as new groups made their appearance they were represented by their most specialized members, the situation for the evolutionists would be, at least, awkward. It would indeed be surprising if the evidences from the sources considered in the preceding paragraphs should be contradicted by the testimony of the rocks. If the rocks contained a full record of all the species that have lived upon the earth their verdict would be crucial, but in considering the history of life as it is revealed to us by fossil forms we should bear in mind that the records are very incomplete. A great many organisms have soft bodies so that they cannot be preserved as fossils. Terrestrial plants and animals are preserved only under very exceptional conditions. Of the birds, mammals, and insects that are living around us, how many will be converted into fossils which may possibly be studied by some future paleontologist? Their bodies, if not eaten by some other animal, simply decay and disappear. In the whole Jurassic period, only two imperfect specimens of birds have been discovered. Doubtless numerous birds, and probably many kinds of birds existed during that period. These particular individuals probably happened to die upon mud flats at low tide, and became buried by a subsequent deposit of sediment as the tide returned. It is only through some peculiar combination of circumstances that such terrestrial forms are preserved in the first place, and it is only by other fortunate circumstances that the rocks containing the remains are exposed so that their contents may be studied. Large parts of the fossiliferous strata of the earth are hopelessly buried under the ocean. Over much of the land the

rocks are buried so deeply as to be practically inaccessible for study. Extensive areas of rocks which once bore fossils have subsequently been metamorphosed by heat so as completely to obliterate all traces of life. Again, the rocks belonging to older epochs have been largely eroded to form the materials for subsequent deposits. The paleontologist must gather his materials where he can and be thankful for what he finds; at best he can obtain but a very fragmentary picture of the vast procession of living forms which have peopled the globe at successive periods of its history.

The early critics of *The Origin of Species* laid great stress upon the absence of connecting links which, it was claimed, ought to be discovered among extinct species of plants and animals. This objection Darwin attempted to meet in advance in his chapter on "The Imperfection of the Geological Record." This record, as Darwin reminds us, is

> a history of the world imperfectly kept, and written in a changing dialect; of this history we possess the last volume alone relating only to two or three countries. Of this volume, only here and there a short chapter has been preserved; and of each page, only here and there a few lines. Each word of a slowly-changing language, more or less different in the successive chapters, may represent forms of life which are entombed in our consecutive formations, and which falsely appear to have been abruptly introduced.

We hear little today about the absence of connecting links as a difficulty for the evolutionist, the reason being that many of them have been found. Much additional knowledge of extinct forms has accumulated since Darwin wrote, and, while the history of life is exceedingly fragmentary, the new discoveries have served partly to fill in many of the gaps in the older records. The widest gap that remains is at the beginning. The Cambrian period, the first subdivision of the Paleozoic era, is the earliest in which fossils are abundantly preserved, but before this time there were laid down deposits of enormous thickness which contain very few indications of organic remains. Most of the

rocks are fresh-water deposits. Some have been metamorphosed by heat, and in others we have only a few algæ, some worm tubes, and scattered fragments of arthropods to attest the

Recent

Quaternary	Pleistocene Period	Man
Cainozoic or Tertiary Era	Pliocene Period	Apes, Pithecanthropus
	Miocene Period	Apes
	Oligocene Period	Higher Placental Mammals
	Eocene Period	Primitive Placental Mammals
Mesozoic Era	Cretaceous Period	Dinosaurs, Toothed Birds
	Jurassic Period	Dinosaurs, Archæopteryx
	Triassic Period	Reptiles, Primitive Mammals
Palæozoic Era	Permian Period	Amphibians, Reptiles
	Carboniferous Period	Abundant Land Plants, Insects, Amphibians
	Devonian Period	Sharks, Ganoids, Land Plants
	Upper Silurian Period	Cartilaginous Fishes
	Lower Silurian Period	Orthoceratites, Armored Fishes
	Cambrian Period	Lower Invertebrates, Molluscs, Trilobites, Corals
Pre-Cambrian Formations	Late Proterozoic	Scant Remains of Lower Invertebrates
	Early Proterozoic	Indirect Evidences of Life
	Archeozoic	Indirect Evidences of Life

FIG. 201—The geological periods and their characteristic forms of life.

presence of life. Grabau states that "from certain lines of evidence it seems that the length of time preceding the opening of the Palæozoic was as great, if not greater than, all the time

which has elapsed since then." In parts of the deposits of this long era the nature of the rocks affords indirect evidence of the presence of living organisms. Whether nearly all of the records of life before the Cambrian are irretrievably lost is uncertain. Thus far, the history of life that has come down to us begins practically with the second half of the story.

When life appears in the Cambrian period, almost all the chief groups of invertebrate animals were already represented. There were sponges, jellyfish, hydroids, corals, worms, molluscs, primitive echinoderms, brachiopods, and large numbers of a group of primitive crustaceans known as trilobites. The next period, the Ordovician, or lower Silurian, shows an advance in many invertebrate types. Cephalopods, which are molluscs related to the present-day chambered Nautilus, were represented by many species, some of which, the orthoceratites, have a straight, chambered shell that sometimes reached several feet in length. At this time we meet with the first indications of fishes in a few remains of a peculiar armored group, the Ostracoderms, which attain their greatest development in the two following periods, the Upper Silurian and the Devonian. During these latter periods there were also introduced fishes allied to our modern sharks and ganoids; and there was a marked advance in many of the invertebrate groups. While the trilobites continued to abound, there were also crustaceans related to our modern shrimps and lobsters. Large animals more or less resembling

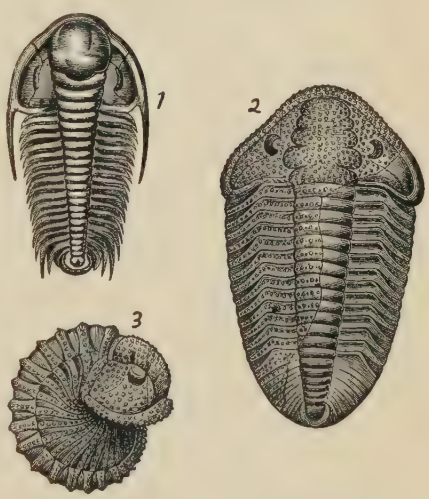

FIG. 202—Trilobites from the Silurian period: *1, Paradoxides harlani; 2, Calymene blumenbachii; 3, Calymene* rolled up and seen from the side. (After Le Conte.)

scorpions and known as eurypterids made their appearance at this time, together with some true scorpions and relatives of our horsehoe crabs. We meet with an advance also in the development of plants. In addition to marine algæ, there were several kinds of terrestrial plants allied to the ferns, club mosses, and primitive conifers; but the most profuse development of plant life occurred in the succeeding, or Carboniferous, period, when

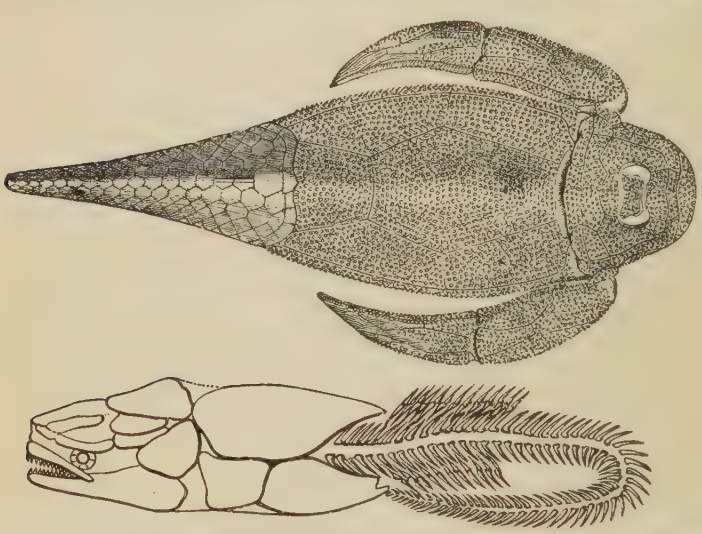

Fig. 203—Armored fishes of the Devonian: the upper figure *Pterichthys milleri;* the lower figure *Coccosteus decipiens.* (After Dana.)

ferns, club mosses, and forms related to the horsetails attained the size of trees and developed dense and luxurious forests. It is in the Carboniferous period that extensive deposits of coal were formed from the remains of these plants. Many cone-bearing trees are found, but the higher types of flowering plants had not yet appeared.

With the advent of forests in the Carboniferous period we meet for the first time with an abundance of insects, although the myriapods, the probable progenitors of insects, appeared in the Devonian. There were a few species of amphibians belonging to orders now extinct. It is probable that amphibians

occurred in the preceding, or Devonian period, but the only indication of their presence is a single footprint. Anyway, it belongs to some large three-toed animal.

The Permian, which is the closing period of the great Paleozoic era, witnessed the differentiation of the group of reptiles. Many of these reptiles were allied to the Amphibia, which at this time were found more abundantly than in the Carboniferous period.

FIG. 204—Carboniferous vegetation. (After Dana.)

Some of the reptiles were allied to the mammals, and, since the earliest mammals date from the next following epoch, the three classes of amphibians, reptiles, and mammals appear to draw more closely together as if converging toward a common ancestral stem.

The Mesozoic era appears to be quite abruptly separated from the preceding Paleozoic. In most countries the rocks of the Triassic, the earliest subdivision, are separated from the last of the Paleozoic by a gap, or break, which indicates the existence of an intervening period of unknown duration. During the Mesozoic era we find no more trilobites, eurypterids, and armored fishes; gone also are the graptolites and the primitive echinoderms known as cystids and blastoids. Brachiopods are

much less abundant, but the molluscs, especially the cephalopods, became more numerous. The coiled ammonites, whose chambered shell recalls that of the modern Nautilus, were represented by very large numbers of species. During this period we find the higher types of bony fishes which largely replaced the more primitive species. The latter part of the Mesozoic saw the appearance of the higher forms of flowering plants. But the most conspicuous feature of this era was the extraordinary development of its reptilian life. This was truly the age of reptiles. The water, the land, and even the air, contained representatives of this dominant group. There were twenty orders of reptiles, only five of which survived in any subsequent era. Most conspicuous among these were the dinosaurs (literally terrible lizards), many species of which attained enormous dimensions. *Tyrannosaurus rex*, a flesh-eating dinosaur, had a length of forty-seven feet, a head over four feet long, and teeth from three to six inches long. The Brontosaurus, one of the largest known dinosaurs, reached a length of over sixty-six feet, and is estimated to have weighed thirty-eight tons. The Diplodocus was a more slender creature, but it attained a greater length, namely, eighty-seven feet. These huge animals were no less remarkable for their size than for their bizarre and ungainly forms. They all had their

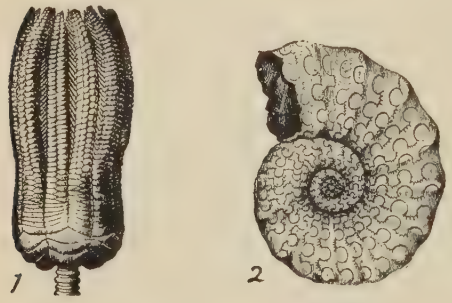

FIG. 205—Mesozoic invertebrates: *1*, a crinoid *Encrinus liliformis; 2*, an ammonite, *Ceratites nodosus*. (After Le Conte.)

FIG. 206—A pterodactyl, an extinct flying reptile. (After H. v. Mayer.)

day in the Mesozoic era, for none of them survived beyond this time.

In the Mesozoic we meet with the first remains of birds. The oldest known representative of this class is the Archæopteryx, of which two specimens only have been found in the Jurassic. These specimens are remarkable in many ways. Unlike modern birds, the Archæopteryx had well developed, conical teeth in both jaws; the tail was much elongated, and composed of a large

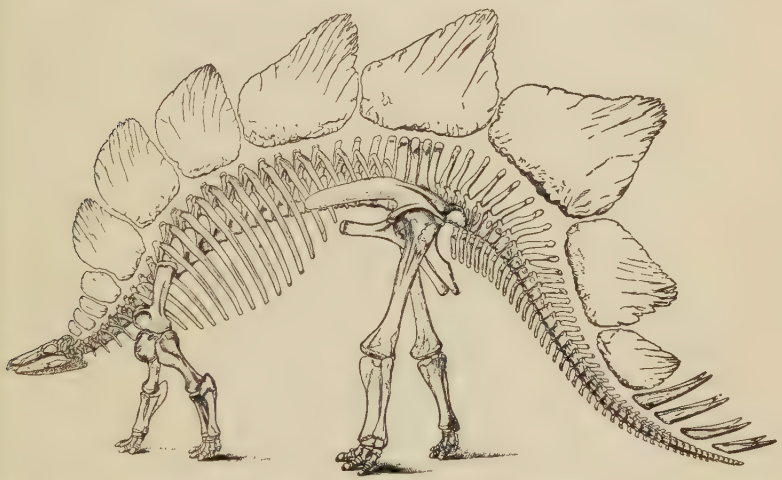

FIG. 207—A restoration of *Stegasaurus ungulatus*, a dinosaur from the Jurassic of Wyoming. (After Marsh.)

number of free vertebræ, into each of which was inserted a pair of large feathers, thus presenting a marked contrast to all existing birds, in which the tail is much shortened and has several of the vertebræ fused into one bone. The wing of the Archæopteryx shows an approach toward the primitive pentadactyl type of limb in having three independent digits, each ending in a claw. Comparative anatomists have long recognized the structural resemblances between birds and reptiles. The discovery of Archæopteryx provides a most interesting link connecting these two classes. There are other toothed birds in the Cretaceous period, which immediately follows the Jurassic, but, aside from

the presence of teeth, they show a fairly close resemblance to modern types (Fig. 210).

The Mesozoic era also saw the first introduction of the mammals. The earliest undoubted remains of this group are found in the latter part of the Triassic, although reptiles with marked mammalian affinities occur in the first part of this period. Throughout the long stretch of the Mesozoic era, the mammals remain small and inconspicuous, most of them not exceeding the size of mice and rats. So long as the reptiles dominated the land, the mammals made relatively little progress; but when the last of the great dinosaurs made their dramatic exit from the

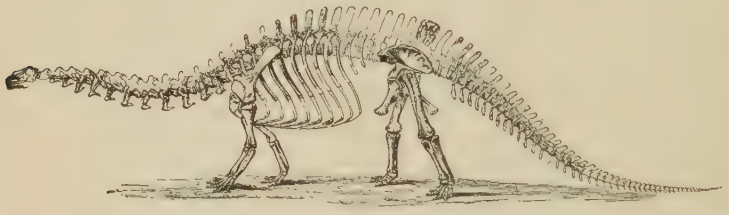

FIG. 208—A restoration of *Brontosaurus excelsus* from the Jurassic of Wyoming. (After Marsh.)

stage of life toward the close of the Cretaceous, the mammals apparently took advantage of their opportunity, and we find them, in the following periods of the Tertiary era, assuming a much larger size, and developing into a large number of diversified forms. The Tertiary is therefore known as "the age of mammals."

The earliest Tertiary mammals contained a considerable number of relatively primitive forms, and some of the orders then represented have since become entirely extinct. Grabau designates them as

> archaic animals with extremely small brains, simple triangular teeth, five-toed feet, and flat-footed (plantigrade) mode of progression. They were defective in mental power, ill-adapted in tooth structure for the effective procurement of food, and in general not well fitted for rapid motion because of their flat-footedness. In other respects, they had become very diverse, simulating the structural characters which in the higher types characterize the different groups.

Fig. 209—The Archæopteryx. Note the clawed digits of the wings, *1, 2, 3.* (After Zittel.)

During the succeeding periods of the Tertiary the mammals made a rapid approach toward modern types. In Miocene times, for instance, there are the remains of deer, camels, rhinoceroses, tapirs, elephants, horses, saber-tooth tigers, and wolves, although most of these forms belong to different genera from those of the present day. During the Tertiary, the flora became much more modernized. As Agassiz has remarked:

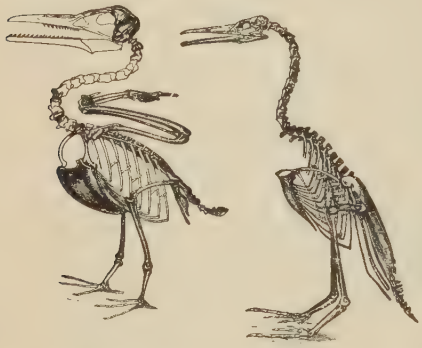

FIG. 210—Toothed birds from the Cretaceous, *Ichthyornis victor* to the left; *Hesperornis regalis* to the right. (After Marsh.)

> The grains, the Rosaceæ with their varied fruits, the tropical fruit trees, Oranges, Bananas, etc., the shade and cluster trees so important to the comfort and shelter of man, are added to the vegetable world

during these epochs. The fossil vegetation of the Tertiaries is indeed most interesting in showing the gradual maturing and completion of those conditions most intimately associated with human life. The earth had already its seasons, its spring and summer, its autumn and winter, its seed time and harvest, though neither sower nor reaper was there; the forests then as now dropped their thick carpet of leaves on the ground in autumn, and in many localities they remained where they originally fell with a layer of soil between the successive layers of leaves,—a leafy chronology by which we read the passage of the years which divided these deposits from each other. Where the leaves have fallen singly on a clayey soil favorable for receiving such impressions, they have daguerreotyped themselves with the most wonderful accuracy, and the Oaks, Poplars, Willows, Maples, Walnuts, Gum and Cinnamon trees, etc., of the Tertiaries are as well known to us as those of our own time.

An important feature of Tertiary plant life was the development of grassy plains over extensive semi-arid regions which appeared at that time in several continents. These plains supported large numbers of grazing animals, the remains of which

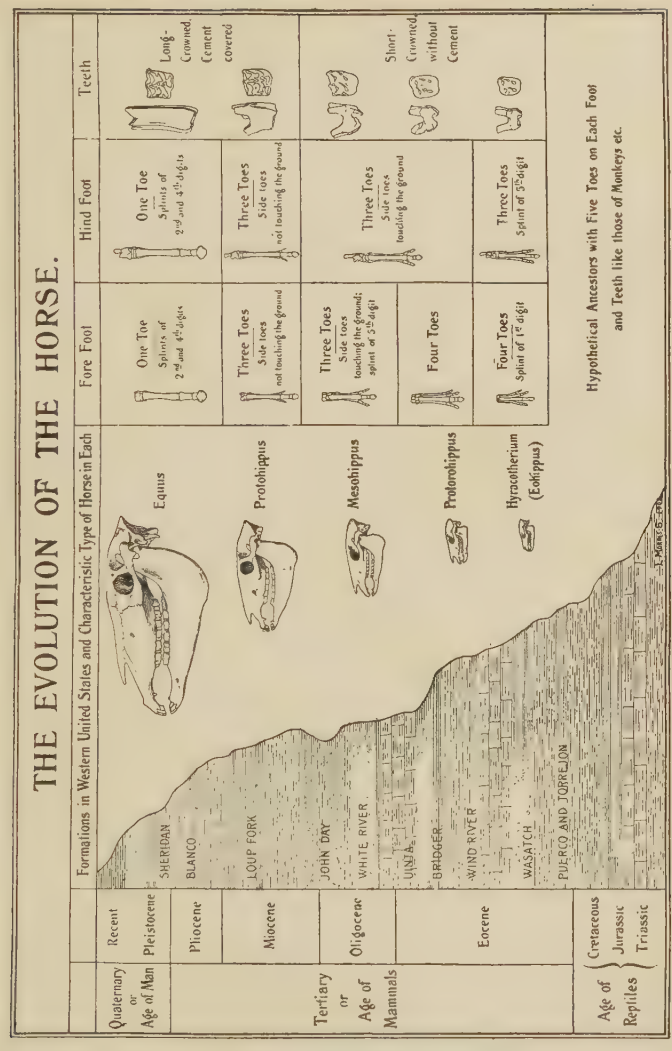

FIG. 211—Stages in the evolution of the horse. (From a Guide Leaflet of the American Museum of Natural History.)

often show striking indications of progressive development as we pass from the earlier to the later subdivisions of the Tertiary era. The most complete series of fossils is furnished by the remains of extinct horses to which we have already briefly referred. Back in the Eocene, skeletons have been found of a little animal, the Eohippus, not larger than a fox. This form represents the earliest known member of a most remarkable series of extinct species which lead to the horses of the present day. The evolutionist would expect, *a priori*, that horses descended from ancestral mammals having the typical number of five digits. The earliest Eocene type approaches this condition in having five digits on the forefoot, and four on the hind foot. In the forefeet the inner digit is represented by only a slender rudiment of the first metacarpal bone, while the outer, or fifth, digit is similarly reduced in the hind feet. The middle digit in both fore and hind feet is significantly larger than the others, a condition which is prophetic of further development in succeeding forms. The neck and limbs of the Eohippus were relatively short, and the teeth were of the primitive and unspecialized type, although the molars and premolars show the beginning of the complicated folds of enamel which characterize the grinding teeth of modern horses.

The small size of these ancient horses need not surprise us, for the mammals of the preceding Mesozoic era were small creatures whose diminutive size may have been useful in enabling them to keep discreetly out of the way of the great reptiles. The succeeding types of horses became larger and larger, and at the same time there was a gradual reduction in the size and number of the lateral digits of the feet, a relatively greater development of the middle digit, an elongation of the neck and legs, a gradual reduction of the fibula and ulna, and a more complicated development of the teeth. Such a large number of the intermediate stages have now been discovered between ancient and modern horses that the series affords an almost conclusive demonstration of the evolution of the horse from primitive, five-toed ancestral mammals. The scene of this evo-

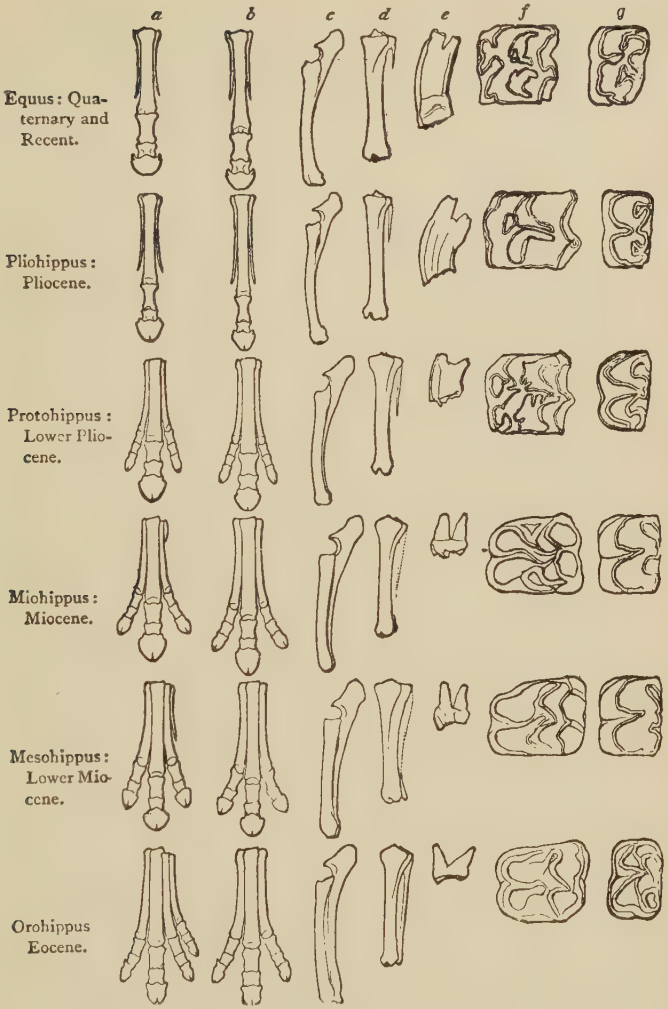

FIG. 212—A series of fossil horses from the Eocene to the present: *a*, forefoot; *b*, hind foot; *c*, radius and ulna; *d*, tibia and fibula; *e*, tooth seen from the side; *f*, *g*, teeth seen from the grinding surface, showing the development of folds of enamel. (After Romanes.)

lution was mainly on the North American continent. Specimens of the old genus Eohippus are found in both Europe and North America, and it is probable that these animals migrated to North America during the Eocene, as they could well have done, by means of the land connection existing at that time across Bering Strait. Horses seem to have died out in the Old World, since we meet with them again only in the late Tertiary when some of the species may have migrated back from North America.

The western plains of North America have yielded remains of fossil horses throughout most of Tertiary time. The Eohippus was followed by Protorohippus, which was a little larger and had no rudimentary first metacarpal. Orohippus and Epihippus, somewhat later Eocene types, showed a further reduction in the size of the lateral digits and a considerable advance in the structural development of the teeth. In the Mesohippus of the Miocene (I am omitting several intermediate types) the digits of the forelegs are reduced to three with a rudiment of a fourth, while there are three digits on the hind feet. The second and fourth digits still retained small hoofs, but in the Pliohippus of the Pliocene these small hoofs had disappeared. In the Pleistocene era, which followed the Tertiary, horses became extinct in both North and South America. The reason for their disappearance is entirely unknown, since, so far as can be ascertained, conditions were not unfavorable for their life. After their introduction by the Spaniards, horses became wild in both the American continents, where they roamed in large herds over the grassy plains.

The series of fossils which speak so strongly in favor of the evolution of the horse does not stand alone. Other series of Tertiary fossils tell a similar story, although the intervening stages are not quite so complete. One remarkable series leads up to our modern species of elephants. These large and curiously organized creatures are apparently quite sharply separated from the other mammals. Although now confined to southern Asia and Africa, elephants formerly roamed over all of the continents

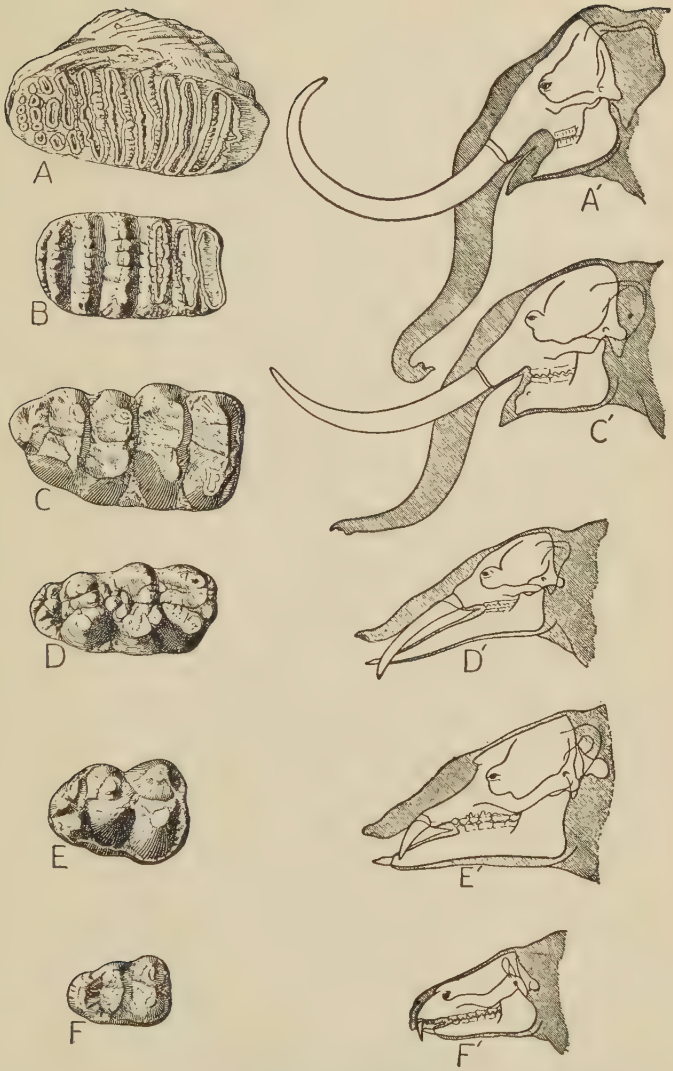

FIG. 213—Evolution of the elephant, showing increased complexities of tooth structure: *A*, *A′*, recent elephant (Elephas) from the Pleistocene; *B*, Stegodon from the Pliocene; *C*, *C′*, Mastodon from the Pleistocene; *D*, *D′*, Trilophodon from the Miocene; *E*, *E′*, Paleomastodon from the Oligocene; *F*, *F′*, Mœritherium from the Eocene. (After Lull.)

except Australia. The earliest member of the elephant series is a small tapirlike animal, the Mœritherium, found in the upper Eocene strata of Egypt. The skull shows only the beginning of that curious elongation of the jaws and enlargement of the tusks which characterizes the later members of the group. The grinding teeth are still generalized in structure, although they possess a number of crests which become very highly developed and specialized in recent species. A somewhat later genus, Palæomastodon, which is also found in Egypt, shows a larger development of the tusks, a marked elongation of the lower jaw, and certain peculiarities of the skull that are indicative of the presence of a proboscis. In the genus Tetrabelodon there is a still greater development of the tusks and lower jaw, and the tooth structure has become more complicated. The genera Dibelodon and Mastodon are characterized by a shortening of the lower jaw and a loss of the lower tusks. Through the intermediate genus Stegodon, the Mastodons are connected with the genus Elephas which contains, in addition to the two living species of elephants, several extinct species including the well known mammoth.

Space forbids the consideration of the series of deer, camels, rhinoceroses, and carnivores which are continually being made more nearly complete by the discovery of new forms. Although the geological record may be very imperfect, nevertheless, so far as it goes, it not only is consistent with the doctrine of evolution, but it has supported this doctrine by a large amount of positive evidence. It has shown that from the period of the earliest organic remains there has been a gradual advance in the various forms of plant and animal life. It has revealed the existence of many types intermediate between existing groups. It has shown that when new groups are introduced they are represented by their more primitive members. It has shown that, as we trace groups back in time, they tend to draw more closely together; and it has afforded several remarkable series of connecting links which throw much light upon the derivation of existing forms. In a word, the whole progress of paleontology has served

to render ever more complete and conclusive the evidence for the doctrine of descent.

The testimony of paleontology as to the origin of man, although much less complete than could be desired, points clearly to the descent of man from some apelike ancestor. No competent morphologist supposes that man was derived from any of the existing species of apes. Man and the apes are considered as representing the ends of a group of branches which lead back to a common stem. People who object to being descended from monkeys may possibly derive some consolation by considering these animals as second cousins instead of progenitors. There cannot be the least doubt, however, that man, apes, and monkeys all belong to the natural order of Primates. Structurally, as Huxley conclusively proved, man differs less from the higher anthropoid apes than the latter differ from the more primitive members of the monkey tribe. But just how man is related genealogically to the various other members of his order is still an unsettled problem.

Remains of the most primitive group of monkeys, the lemurs, are found as far back as the Eocene. In the Oligocene, remains of an anthropoid related to the modern gibbon have been found in Egypt. Other apes resembling the anthropoids occur in the middle Miocene, while during the Pliocene the anthropoids are represented by forms that more or less closely resemble the existing species of chimpanzee, orang-utan, and gorilla. The anthropoids died out relatively early in Europe, but they have persisted in Africa and parts of southern Asia.

In 1894, the Dutch surgeon, Dubois, described parts of the skeleton of an apelike human being, *Pithecanthropus erectus*, which was discovered in the late Pliocene, or early Pleistocene deposits of Java. Of the head only the upper part of the skull and two molar teeth were preserved. The forehead was low and flattened, and had a projecting brow. The cranial capacity was about two-thirds that of an average human skull. The teeth are described as being more human than apelike. A single femur, which was found about fifty feet from the rest of the

skeleton, indicates, if it really belongs to the same skeleton, that the Pithecanthropus must have been nearly as tall as the average European. What is known of Pithecanthropus indicates that it represents a very primitive type of human being, or a very human type of ape, whichever we may be pleased to call it.

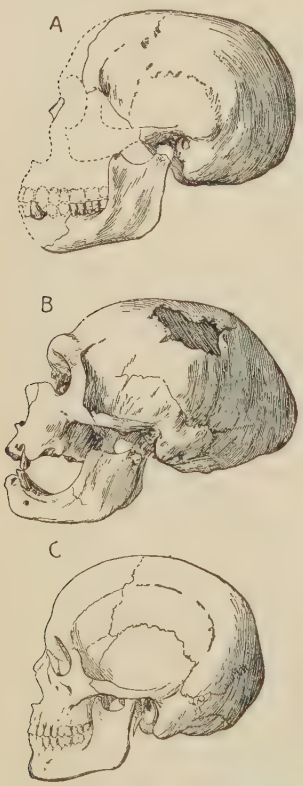

FIG. 214—*A*, skull of the Piltdown man; *B*, skull of a Neanderthal man from La-Chapelle-aux-Saints; *C*, modern human skull. (By permission of the Geological Society of London.)

Next in age to Pithecanthropus (which is supposed to date back nearly 500,000 years) comes the Heidelberg man, of whom only a single lower jaw was discovered about seventy-nine feet below the surface near Heidelberg, Germany, with the remains of several extinct animals. The teeth are described as distinctly human, but primitive; but the jaw is unusually massive and apelike, and devoid of the distinctively human projecting chin (Fig. 215C).

Another primitive human type is the Piltdown man discovered in Sussex near the river Thames. The cranium was of fair size, but if the lower jaw found near by really belongs to it and not, as has been suggested, to a chimpanzee, the Piltdown remains probably belonged to a creature sufficiently below present-day man to justify the institution of the separate generic name of Eoanthropus (literally "dawn man"). According to Prof. Elliot Smith, the claim that the lower jaw belonged to a chimpanzee "ignores not merely the improbability of such a chance association in the same spot of the remains of a hitherto unknown man-like Ape, and an equally unknown ape-like Man, one of which left his skull without the jaw, and the other the jaw with-

out the skull, but also the large series of anatomical peculiarities of the jaw and teeth which prove the jaw to be, not a chimpanzee's, but that of a primitive human being—no doubt a part of the same individual whose skull was deposited alongside it."

The Rhodesian skull found a few years ago in South Africa shows also a well developed cranium, but this is associated with facial peculiarities which indicate that the face belonged to a type "more primitive and brutal than any other human being, living or extinct, that is at present known" (Smith). It is apparently impossible to specify, with any degree of accuracy, the precise period of time to which either the Piltdown or the Rhodesian skull belongs.

The celebrated Neanderthal skull belonged to a race of primitive men with a low, flattened cranium, short flexed legs, and short, thick set body, who ranged over a considerable part of Europe. *Homo neanderthalensis* was probably not a particularly prepossessing species of his genus. According to Osborn, "the cranium is dolichocephalic, with prominent supraorbital processes and relatively short and broad nose, weak lower jaw, lacking the prominent chin process. These characters, as well as the posterior position of the foramen magnum and the form of the palate, are distinctively simian or prehuman."

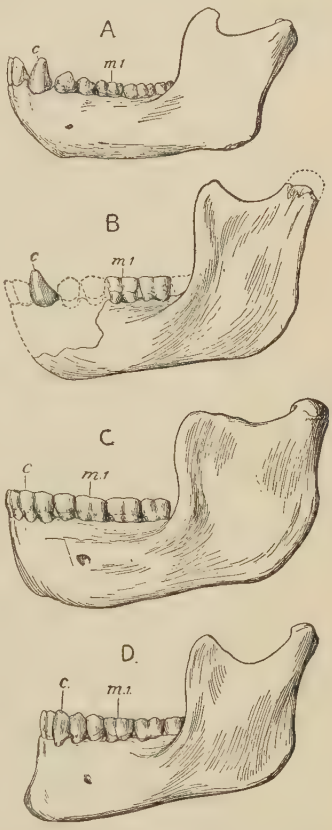

FIG. 215—Lower jaw of—*A*, chimpanzee, *B*, Piltdown man, *C*, Heidelberg man, *D*, modern man; *c*, canine tooth; *m. 1*, first molar tooth. (Courtesy British Museum and Geological Society of London.)

Neanderthal man was succeeded by the Crô-Magnons, who

were a fine, tall people with high foreheads and well developed crania. Their remains, together with specimens of their handiwork, are found widely scattered over Europe and parts of western Asia. The Crô-Magnons were followed by several other races whose history has as yet been very imperfectly traced.

G. THE EVIDENCE FROM GEOGRAPHICAL DISTRIBUTION

It is perhaps not immediately evident that the study of the way in which species of plants and animals are distributed over the surface of the globe, should afford a most excellent means of judging whether or not they arose by a process of evolution. The significance of paleontology for evolutionary theory is obvious enough. The distribution of organisms in time, as we have seen, is in close agreement with what would be expected according to the theory of descent. But the distribution of organisms in space is no less important in relation to evolution, and its verdict no less crucial.

We may perhaps make this fact more obvious by employing an illustration from an imaginary case. Let us suppose that during the history of the earth's surface only a single large island should have arisen out of the sea. This island, we may suppose, was peopled by organisms which left their original aquatic habitat and gradually became adapted to a terrestrial mode of life. In accordance with the doctrine of evolution let us further suppose that these original inhabitants gave rise through descent to a diversified fauna and flora, the species of which became scattered over its surface and settled down in situations to which they were peculiarly fitted. We may assume also that our island was the scene of many geological changes; mountain chains were erupted at various periods, dividing it into regions across which most species were unable to migrate. Through the subsidence of certain areas, parts of the island were cut off from the mainland at different stages of its history, thereby forming smaller islands whose inhabitants were isolated for varying periods of time. Remember that, during all this time, life was evolving, and species were branching and rebranching from the

original ancestral forms and migrating where they could. What kind of a picture would the distribution of species on our island present?

If a naturalist (who, we may assume, is a geologist as well as a botanist and zoölogist) should visit this region and study its fauna and flora in order to find some clue as to their possible evolution, what sort of relations would he look for? Among other things he would certainly study the relation of barriers to the distribution of the species which they separate. He would expect to find that those regions which had been separated for the longest time would have the most widely different forms of life. If he studied the geological history of the outlying islands and ascertained the relative periods at which they were cut off from the mainland, he would look for the greatest differences in the life of those which had been first formed. Our naturalist would doubtless anticipate that the area occupied by a species would be closely related to its means of dispersal. He might look for slow-burrowing moles, for instance, to be quite restricted in the range of their species, while the species of ferns or fungi, whose spores could be easily carried to great distances by the wind, would be found in almost every locality suitable for their growth. He would also probably infer that closely related species would exhibit a tendency to cluster together more or less in the same general area. And since, according to the theory of evolution, present species are the descendants of previously existing ones, our naturalist would seek in recent deposits forms similar to those now living in the same region.

All of these relations which the naturalist would look for would inevitably exist in our island area if its fauna and flora had arisen by a process of evolution. Consequently if the naturalist discovered that these relations actually existed, he would be pretty sure that evolution had taken place. If, on the other hand, the various species had been created, there would be no assignable reason why most of these relations should be found.

Our illustration ought to make it apparent, I think, that a study of the distribution of species over the earth should afford

abundant means of critically testing the theory of evolution. If the theory be correct it should supply the key to understanding many phenomena of distribution which would be otherwise unintelligible. If it affords this key the presumption in favor of its truth would be very great.

Mr. Darwin seems to have been the first man who adequately grasped this general fact. In his two chapters on "Geographical Distribution" in *The Origin of Species* he showed how the salient features of distribution receive a natural and rational explanation according to the theory of evolution. It is a familiar fact that the great continental regions of the earth possess their own peculiar types of fauna and flora. Students of distribution divide the earth's surface into five or six principal regions, each of which is subdivided into several minor areas. The main regions usually adopted are (1) the Palæarctic, which includes Europe and Asia north of the Himalaya Mountains, and Africa north of the Tropic of Cancer; (2) the Nearctic, or North America with the exception of Central America and a part of Mexico; (3) the Neotropical, or South America plus the aforesaid areas of Central America and Mexico; (4) the Ethiopian which includes the part of Africa south of the Tropic of Cancer; (5) the Oriental, consisting of India, Indo-China, and some of the islands to the south and east; and (6) the Australian, which includes Australia and some of the outlying islands mainly to the north and east of the continent.

On account of the general similarity of their faunas and floras the Palæarctic and Nearctic regions are sometimes united into a single region called the Holarctic. In both Europe and North America we find related but generally distinct species of bears, wolves, wild cats, foxes, weasels, squirrels, hares, rabbits, deer, moles, and otters. In the forests of both continents we meet with oaks, sycamores, willows, maples, and alders; and among the smaller flowering plants there is a large number of allied species. A few families represented in North America—namely, those including the opossums, humming birds, and prairie dogs—are not found in Europe. Nevertheless, students of dis-

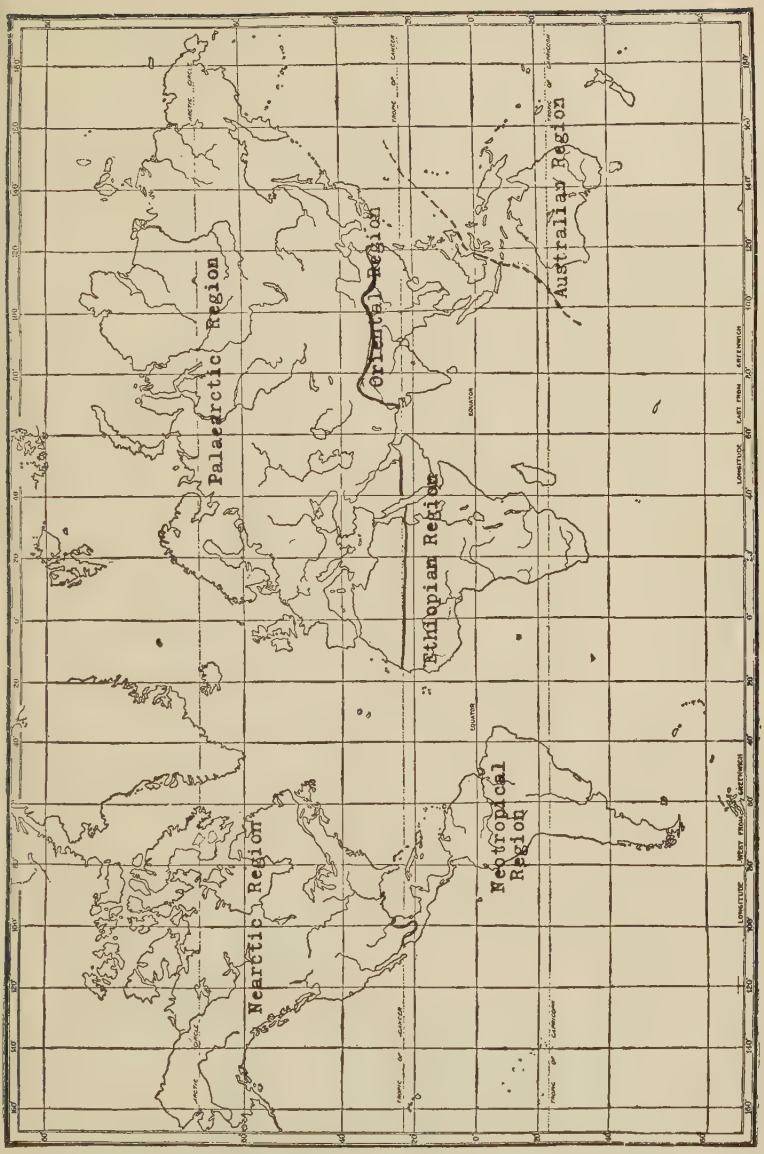

FIG. 216—The chief geographical regions. The broken line between Asia and Australia represents Wallace's line.

tribution are abundantly justified in regarding the Palæarctic and the Nearctic regions as more closely related than any two of the other great geographical areas.

When we compare the regions lying in the southern hemisphere we find a very different situation. In the continent of South America there is a marvelous wealth of unique forms of plant and animal life. Among the mammals, to mention only a few outstanding examples, there are the llamas and alpacas, sloths, anteaters, armadillos, agoutis, peccaries, bloodsucking bats, and prehensile-tailed monkeys. In the bird fauna, which includes an unusually large proportion of brilliant and conspicuous forms, there is a very large number of peculiar species, "a series of types," according to Wallace, "more varied and more distinct from those of the rest of the world than any other continent can boast of." The reptiles, amphibians, fresh-water fishes, and insects consist also of species usually found nowhere else in the world.

If now we pass across the Atlantic to the Ethiopian region we shall be introduced to a distinct new world of life. The larger mammals are very different from those of South America. Instead of the prehensile-tailed monkeys, which belong to a unique subdivision of the Primates, we find, on the one hand, the baboons and the large anthropoid apes such as the gorilla and the chimpanzee, and, on the other, the group of lemurs which occurs nowhere in the Western Hemisphere. While bears, deer, and wild oxen are conspicuous by their absence, there is an unusually large proportion of large quadrupeds, which include the elephant, rhinoceros, hippopotamus, giraffe, lion, leopard, zebra, okapi, wild ass, and numerous species of antelopes. The bird fauna is no less rich and unique, and there are large numbers of peculiar species of reptiles, fishes, insects, and land shells.

Taking a voyage to Australia, we encounter a fauna and flora still more unique. The mammals, with the significant exception of some bats and a few species introduced by man, consist exclusively of marsupials and monotremes. Mammalian life in Australia has become diversified in ways which more or less

closely parallel the subdivisions of the higher, or placental mammals of other regions. There are the herbivorous kangaroos, the burrowing marsupial mole, the wolflike Tasmanian tiger, the climbing phalangers, the ant-eating Myrmecobius, and other forms whose habits resemble those of rabbits, squirrels, and marmots. The curious egg-laying duckbill, which lives a semi-aquatic life, and the spiny ant-eaters, which are found chiefly in rocky districts, are the only living representatives of the primitive order of monotremes, and they are all confined to the Australian region. In its bird fauna Australia has more in common with other regions, especially the Oriental, but, as remarked by Wallace, "there are no vultures, woodpeckers, pheasants, bulbuls, or barbets in the Australian region; and the absence of these is almost as marked a feature as that of cats, deer, or monkeys, among the mammalia." On the other hand, there are many birds which are confined to the Australian region, *i. e.*, the lyre birds, honeysuckers (a peculiar family), the mound-building megapodes, which are the only birds that never sit upon their eggs, the ostrichlike emus and cassowaries, and (in New Guinea) the gorgeous birds of paradise.

FIG. 217—The Tasmanian wolf. (After Flower.)

FIG. 218—The Australian duckbill. (After Gould.)

If we attempt to understand why these three great regions of the Southern Hemisphere differ so profoundly in their inhabitants, it is evident that we cannot explain the facts as a

result of difference of soil or climate, since within each of these regions there are differences as great as those we should encounter in passing from one continent to the other. Neither can it be maintained that each region is inhabited by the species that is best suited to thrive in it. Since their introduction into Australia and New Zealand, rabbits have increased so rapidly as to become a serious nuisance. Horses and cattle have multiplied enormously since they were transported to North and South America, and the spread of the English sparrow in the United States is notorious. A considerable part of the flora that occurs along the roadsides and in cultivated fields of every country consists of plants which have been artificially introduced. A number of our worst weeds are invaders from abroad, and many imported insect pests, such as the gypsy moth, codling moth, and red scale, have proven so prolific and destructive that a strict watch is kept at our ports of entry in order to prevent other possible pests from gaining access to the country. A long list could be made of introduced forms which have more or less completely exterminated the native species with which they came into competition. There is abundant evidence, therefore, that countries are not peopled by the species best adapted to live in them.

How then shall we account for the differences in the life of our geographical regions? The special creationist has no explanation to offer beyond the assertion that, for some inscrutable reason, the Deity chose to create species in certain localities, and this, to say the least, is not very illuminating. Why the 400 or more species of humming birds should be confined to North and South America, or why the faunas of England and the European continent should be so similar, whereas those of the near-by islands of Borneo and Celebes should be so different, are matters upon which the creationist is unable to throw a single ray of light. It is only when phenomena are due to natural causes that they are susceptible of a scientific explanation. The evolutionist in grappling with the problems to which we have referred is led to study the geological history of the regions

in question, the length of time they have been separated, and the means by which they could be stocked with animal and plant life. The general similarity of the life of North America to that of Europe and northern Asia is readily explained by the fact that these continents are grouped closely together in northern latitudes. In the very recent times, geologically speaking, Asia and North America were broadly connected across Bering Sea, so that free opportunity was offered for the migration of species from the one to the other. South America, on the other hand, was isolated from the North American continent for a long period during the mid-Tertiary, although it was previously, as well as subsequently, connected by a much broader belt of land than at the present time. For a long period the life of South America developed in isolation from the rest of the world. Hence we can well understand its large number of peculiar forms.

The Ethiopian region likewise had its long period of isolation. For a considerable part of the Tertiary its previous connection with Europe and Asia was interrupted. Later it was joined to Asia across the Red Sea and to Europe across the Mediterranean. The life of Africa, therefore, had an opportunity to develop in its own way during a large part of its history. The same is true to an even greater degree of Australia. In the early part of the Eocene period the Australian region was united by a broad belt of land with Asia. This connection was broken during the middle Eocene and has remained so ever since. Australia could therefore receive only such land mammals as were developed during this early part of the Tertiary. These, as might be expected, consisted, apparently, only of marsupials and monotremes, which were the presumable ancestors of the present mammalian fauna.

The doctrine of evolution, therefore, when interpreted in the light of previous geological history, affords a perfectly natural and rational solution of our problem. It also explains the fact that the extinct species of our several regions present a marked affinity with the living species of the same areas. Darwin noted in the recent deposits of South America that there were many

species of fossil edentates related to the living remnants of that limited order found in the same region. The fossil mammals of Australia, with the exception of recent remains of the dingo dog which was probably introduced by the natives, consist of marsupials and monotremes. And the remarkable wingless birds of New Zealand were preceded by more numerous extinct relatives, one of which, the Dinornis, which reached a height of eleven feet, was the largest of known fossil birds.

The relation of antiquity of barriers to differences in the inhabitants of the separated areas is of sufficient importance to deserve some further illustrations. Let us consider the large island of Madagascar, which lies about 250 miles to the east of South Africa. The fauna of this island is highly peculiar, although it exhibits affinities with that of Africa and also with that of the Oriental region to the northeast. The characteristic large animals of Africa are singularly lacking. There are no elephants, apes, giraffes, lions, zebras, wild asses, or hyenas, and not a single representative of the group of antelopes found so abundantly on the mainland. Instead, we encounter an extraordinary profusion of species of lemurs, a group much more sparsely represented in Africa, India, and the Malay Archipelago. There are several species of insectivores, a few species belonging to two mammalian families found nowhere else in the world, some rats and mice, a semi-aquatic river hog, and a small hippopotamus. More than two-thirds of the birds are peculiar to the island, and the other forms of life present a high percentage of peculiar species. According to several authorities, Madagascar probably had no connection with the continent of Africa later than the middle of the Tertiary. It received, therefore, the rather primitive mammalian fauna which had appeared up to that time. The larger African mammals, which probably invaded the country from the north during the later part of the Tertiary, were prevented from entering Madagascar, whose fauna, like that of Australia, has developed for a long period in isolation.

A case equally remarkable is afforded by the large islands of

New Zealand. Lying about 1200 miles east of Australia, the nearest mainland, New Zealand is much isolated from the rest of the world, and the unique character of its fauna and flora bespeaks its long separation from any continental region, if, indeed, it was ever connected with any other extensive land area. With the exception of bats, there are no mammals there which are known not to have been introduced by man. Most of the birds and all of the reptiles are peculiar to the island, the remarkable lizard-like Sphenodon representing the only survivor of a very ancient order.

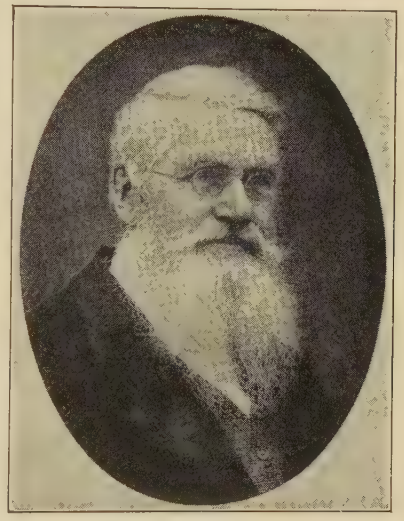

Fig. 219—Alfred Russel Wallace.

The importance of antiquity of barriers in enabling us to understand the peculiarities of distribution is nowhere better exemplified than in the Malay Archipelago. There is a line known from its discoverer as Wallace's Line extending among the islands of this region, which was held by Wallace and some other students of distribution to mark the separation of the Australian from the Oriental region. This line runs between Borneo and Celebes and two smaller islands, Bali and Lombok, which are separated by a deep strait only fifteen miles wide in its narrowest part (Fig. 216). Yet, Wallace remarks,

these islands differ far more from each other in their birds and quadrupeds than do England and Japan. The birds of the one are extremely *unlike* those of the other, the difference being such as to strike even the most ordinary observer. Bali has red and green woodpeckers, barbets, weaver-birds, and black-and-white magpie-robins, none of which are found in Lombok, where, however, we find

screaming cockatoos and friar-birds, and the strange mound-building megapodes, which are all equally unknown in Bali. Many of the kingfishers, crow-shrikes, and other birds, though of the same general form, are of very distinct species; and though a considerable number of birds are the same in both islands, the difference is none the less remarkable—as proving that mere distance is one of the least important of the causes which have determined the likeness or unlikeness in the animals of different countries.

Again, Cuba and Florida, although separated by a narrow strait about fifty miles in width, and having much the same semi-tropical climate, nevertheless, have remarkably different floras and faunas. To quote Wallace once more, "Between frigid Canada and sub-tropical Florida there are less marked differences in the animal productions than between Florida and Cuba or Yucatan, so much more alike in climate and so much nearer together."

In both the preceding instances the barriers separating near-by regions are of great antiquity. All over the world we meet with similar examples of the principle that the key to understanding the present distribution of organic forms is to be found in the past geological history of the regions they inhabit. This is what we should expect according to the theory of evolution. It is quite unaccountable according to the opposed theory of creation.

It is evident, *a priori*, that the area occupied by a species should be in part determined by its means of dispersal. Different kinds of organisms have very unequal opportunities for rapid diffusion. The dried cysts of protozoöns, and the spores of molds, mosses, and ferns, may be blown to great distances by the wind, and accordingly we find that the distribution of a considerable proportion of these forms is nearly world-wide. They are limited mainly by barriers of climate, or other conditions affecting their growth. The seeds of some of the flowering plants have special devices which enable them to be carried for considerable distances by the wind. Other seeds may float for many days or weeks in sea water without losing their power of germination. Seeds may be carried in the dried mud on the

feet of birds. During their migrations birds may fly to great distances, and they are occasionally blown by hurricanes even across the Atlantic. Many seeds eaten by birds pass through the body without injury. In one way or another, therefore, birds may greatly aid the distribution of plants, and they may carry also many of the smaller forms of animal life. Insects are often blown out to sea for several hundred miles, and small spiders, buoyed up by their masses of web, have been observed to settle on ships over 150 miles from land.

Another means of transportation is afforded by means of driftwood and the large floating masses of vegetation which are occasionally carried out to sea, especially in the tropics, by rivers. Sometimes these islands which have floated down from some of the large rivers of South America have been carried several hundred miles from shore. On one occasion a boa constrictor was borne on a large floating tree from South America to the island of St. Vincent, where it destroyed some sheep before it was found and killed. The fact that reptiles usually lay eggs which can be transported in masses of soil on floating islands considerably facilitates the distribution of these forms. It is perhaps for this reason that reptiles are much more widely scattered among the islands of the earth than either the mammals or the amphibians.

A study of means of dispersal is of a special importance for understanding the distribution of life upon islands. In regard to their origin, islands are divided into two classes, the continental and the oceanic. The first kind originated by being separated from the mainland through the subsidence of the intervening region. From their beginning they were already stocked with living forms, although they have doubtless received many additions since their separation. The oceanic islands are those which at no time were connected with any large continental area. They were born, like Aphrodite, out of the sea. Frequently they are very remote from any mainland. They are generally the product of volcanic action, although in many cases they are formed partly of coral. Except for the occasional

transformation of marine animals, which, like the coconut crab, have become adapted to terrestrial life, we should expect oceanic islands to be stocked only by stray visitors, the flotsam and jetsam of the organic world, that happened to be stranded on their shores. And the character of their inhabitants is in accordance with this expectation. This is a matter of great significance in relation to evolutionary theory, for if we should find elephants, giraffes, and anthropoid apes indigenous to such out-of-the-way islands as St. Helena or Hawaii and other places to which these animals could not have been carried by any known means of transportation, the evolutionist would be sorely worried. Of course the evolutionist has plenty of puzzling problems of distribution; but if species were miraculously created it seems evident that there would be many instances of distribution which could not possibly be explained as the result of any imaginable natural process. But there are not only no elephants on oceanic islands; there are practically no other mammals. It is true that there are some exceptions, but they are of the kind that prove the rule, since they are chiefly either bats, which could reach the islands by flying, or rats and mice, which, if not carried by ships, as they are known to have been in several cases, might possibly have been transported by floating driftwood or rafts of vegetation.

As Darwin pointed out, oceanic islands are characterized by an equally prevalent absence of amphibians. When these animals are introduced upon oceanic islands they commonly thrive there, as is illustrated by the rapid spread of toads in Bermuda and of frogs in Madeira, the Azores, and Mauritius, where they have multiplied so as to become a nuisance. I think it is safe to say that in all the multitudinous phenomena of distribution there are no cases which cannot reasonably be accounted for without invoking the aid of any but the natural means of dispersal which have been observed in operation.

The faunas and floras of oceanic islands are usually meager. They are characterized by a high percentage of peculiar species, which is probably the result of the long isolation of their in-

habitants and the fact that the islands were originally stocked by a relatively few individuals. But, however unique their forms of life may be, they show a general affinity to those of the nearest mainland. A typical illustration is afforded by the Galapagos Islands, a group of volcanic origin situated under the equator nearly 600 miles west of South America. It is a noteworthy fact that these islands were visited by Darwin during his voyage around the world in the Beagle, and that the study of the peculiar distribution of the species found there and their relation to those on the mainland was one of the principal causes that led Darwin to doubt the fixity of species. Although "almost every product of the land and of the water bears the unmistakable stamp of the American continent," the islands show a very unusual number of types found nowhere else in the world. Of the land birds, all but two are peculiar to the islands. A very curious feature of the fauna is the prevalence of the large land tortoises, of which there are fifteen species. For the most part, these are confined each to a single island. There are eight species of lizards of the genus Tropidurus, no two of which inhabit the same island of the Archipelago. The extent to which the various islands of the group have their peculiar species related to, but distinct from, those of neighboring islands is one of the outstanding features of the fauna of the Galapagos, and one which is indicative of the influence of isolation on the formation of distinct species.

A very instructive illustration of how oceanic islands receive their living inhabitants is afforded by the island of Krakatoa. During a volcanic eruption in 1883 a part of the island was submerged, and the rest was covered so thickly with lava and ashes as completely to destroy all traces of organic life. Three years later a multitude of blue-green algæ was found on the rocks, together with 11 species of ferns and 15 species of flowering plants. In 1897 there were 12 kinds of ferns and 50 of flowering plants. By 1906 the species of flowering plants had increased to 114. The island became gradually stocked also with animals. In 1889 several kinds of beetles, bugs, butterflies, flies, and even

a lizard were found. A study of the fauna in 1908, twenty-five years after the eruption, resulted in the discovery of 263 species, of which 240 were arthropods, 4 land snails, 2 reptiles, and 16 birds. By 1920 the number of species had increased to 573, among which were 26 birds, 1 snake (a python), and 3 mammals (2 bats and a common house rat). All of the plants and animals were found to consist of species occurring in neighboring areas.

It is a general principle of distribution of the greatest importance and significance that closely allied forms tend to cluster in the same general region. As Wallace remarks, "Every species has come into existence coincident both in space and time with a preëxisting and closely allied species." This is, of course, what we should expect if species were derived the one from the other. We should also expect a certain amount of correspondence between the degree of structural similarity in organisms and their degree of proximity in space. If we imagine organisms gradually diverging from each other and becoming divided into species, genera, and families in the course of their descent, we should expect the newly arisen groups (the smaller subdivisions) to occur in neighboring areas. As they diverge more widely in structure they would naturally become more widely scattered.

The general affinity between the inhabitants of the same geographical region is therefore readily explained as the result of a common descent. Very frequently the members of the same genus are confined to the same restricted area, as is abundantly illustrated in island faunas. All but three of the twenty-eight genera of terrestrial mammals in Madagascar are peculiar to the island. More rarely do we find a limited range of the members of a family. The opossum family and the humming-bird family are confined to the New World. On the Sandwich Islands there is a large family of land shells, the Achatinellidæ, consisting of over 300 species and numerous varieties found nowhere else in the world. The numerous varieties and species of this family are frequently confined each to a single valley, the nearest valleys furnishing the most closely allied forms. The Sandwich Islands also possess a peculiar family of birds,

the Drepanidæ, consisting of nine genera and about forty species. Some species have a short, massive bill like that of a parrot; in some the bill is short and slender, and in several others it is long and curved downward. The striking modifications of form and habit occurring in this family recall the diversities of the marsupial fauna of Australia. The group is probably an ancient one which, in the absence of much competition from other kinds of birds, has branched out and become adapted to live in a number of different situations.

In a very high percentage of cases, the members of a species have a continuous range. Exceptional cases occur where a once widely ranging species has become extinct in parts of its former area of distribution. The Torrey pine of California presents such a case, since it is found only in a small grove on the mainland near San Diego and on some of the small islands off the coast of southern California. Often, but less frequently, the species of a genus have a continuous range, or a range broken by relatively narrow barriers. The same principle applies in decreasing degrees to the genera of a family, the families of an order, and the orders of a class. It may be regarded as the expression of the tendency of groups of organisms to remain somewhere near their place of origin.

There are, however, striking cases of discontinuity and a consideration of these is instructive in affording further insight into the agencies which affect the distribution of species. On the top of the Alps, Pyrenees, and Caucasus Mountains there occur several identical or closely related species which are not found in the intervening areas. In some cases these are the same as, or closely related to species inhabiting the Arctic Zone. The explanation of these cases of discontinuity is afforded by the fact that during the last glacial period an immense sheet of ice gradually extended from the polar regions, driving ahead of it the flora and fauna of the continent. With the subsequent retreat of the ice sheet, species adapted to live in a cold climate followed it back and also ascended the mountains, so that they now survive only in these widely separated localities.

Other discontinuities of distribution are accounted for by the extinction of ancestral forms in intermediate regions. Marsupials are now found only in the Australian region and in the New World, but remains of marsupials occur in the early Tertiary deposits of Europe and Asia, as well as in North and South America. Similarly the tapirs, which are now represented in South America and southeastern Asia, were formerly found in Europe, China, and North America. The camel family, which at present is native only in Asia and South America, is found in the Tertiary and later formations of North America, Asia, and Europe. Also the monkeys, to come nearer home, are found only in the Ethiopian region, the Neotropical region, and in Asia, but, as we have seen in the previous section, monkeys were found during the Tertiary in North America and Europe as well as in the continents they now inhabit.

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CHAPTER XVII

HOW IS ORGANIC EVOLUTION CAUSED?

The present chapter deals with several topics of a more or less controversial nature. There is practically no difference of opinion among informed scientific men as to whether or not evolution has taken place. That is no longer a live issue. But there is a good deal of difference of opinion as to how and why evolution may have been brought about. The evidences for evolution are perfectly cogent, even though all theories as to how the process of evolution might have been caused should be swept away. No one doubts the fact of embryonic development, although if a biologist were asked to explain why a frog or a chick develops from a fertilized egg, I fear that he could not give a very satisfactory reply. Although embryonic development is a familiar phenomenon, we seem to be actually much farther from explaining why it occurs than we are from accounting for the evolution of species.

Lamarck, as we have seen, attributed organic evolution mainly to the transmission of characters acquired by organisms in adjusting themselves to their environment; but, for the reasons that have been stated, most biologists regard the Lamarckian factor alone as incapable of affording a satisfactory explanation of evolution, and a great many biologists reject it entirely. The theory which has received the widest recognition as offering a probable explanation of evolution is that of natural selection, which was advanced independently by Charles Darwin and Alfred Russel Wallace.

The idea of natural selection was suggested to both Darwin and Wallace after reading Malthus' celebrated *Essay on Population*. The chief thesis of that able essay is that human population tends to increase faster than its means of support, and that

it is consequently kept within bounds by various checks, among which are war, pestilence, and famine. The pressure upon the means of subsistence that results from this overmultiplication inevitably leads to a struggle for existence which, for a large part of mankind, has been more or less severe as far back as human history has been traced. Darwin and Wallace carried over the doctrine of Malthus into the world of plant and animal life. All organisms, it was pointed out, tend to multiply at a geometrical rate of increase. There must inevitably be a struggle for the necessities of life. Many organisms must perish for lack of adequate means of support. A female codfish lays nearly 10,000,000 eggs, but only two on the average produce fishes which reach adult age. It has been estimated that if all the progeny of an oyster could be saved for only four generations the shells would make a heap eight times the size of the earth! Under such conditions competition must indeed be keen.

The ideas which Darwin and Wallace added to the doctrine of Malthus were those of variability and selective survival. It is a familiar fact that organisms vary. Among the variations there will naturally be some which are better adapted to meet the conditions of life than others, and these on the average will be preserved. Given hereditary variations subjected to the struggle for existence, there will result what Spencer has termed in his famous phrase, "the survival of the fittest." This whole process of selective survival of the fittest hereditary variations is called natural selection.

The term natural selection was chosen to desiginate a certain similarity between selection, as it was conceived to take place in nature, and the artificial selection carried on by the breeder of plants and animals in order to effect the desired improvements of his stock. If a breeder is endeavoring to produce a superior variety of race horses he breeds from those animals having the highest record for speed. Our modern race horse is a specialized product of many generations of selective breeding. Similarly, the strong and heavy draft horse represents a product of selective breeding for very different qualities. Through selection. the

yield of milk in domestic cattle has been increased to a remarkable degree; in the same manner there has been brought about a marked improvement in the yield of wool in sheep, the egg-

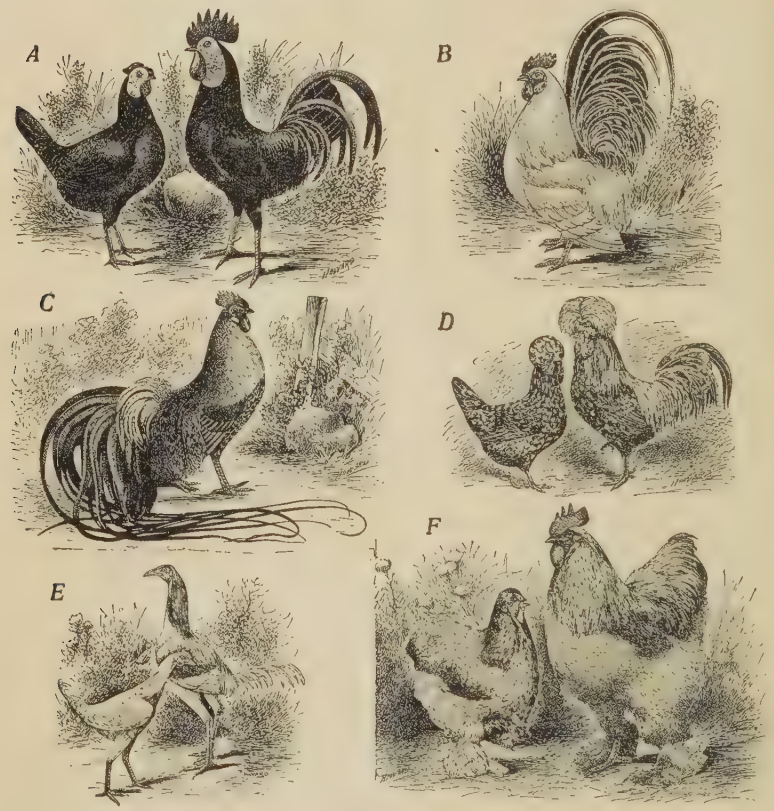

FIG. 220—Breeds of domestic fowls, showing the results of crossbreeding and selection: *A*, white-faced black Spanish; *B*, black-tailed Japanese bantam; *C*, long-tailed Japanese game fowl; *D*, Houdins; *E*, red Pyle games; *F*, buff Cochins. (After Howard.)

laying capacity of the domestic fowl, and the quality and yield of grains and fruits. The work of the selective breeder has been greatly facilitated by crossing related varieties in order to secure the variations among which the desired selections can be made. It is in this way that Mr. Burbank has accomplished most of

his remarkable achievements in the breeding of plants. In this way there has arisen the manifold variety of dogs which exhibit such diverse types as the terrier, the poodle, the King Charles spaniel, the greyhound, the bulldog, and the St. Bernard. Dogs arose from several wild ancestral varieties or species, and they have been crossbred and selected, consciously or unconsciously, for very diverse qualities. Our horses, cattle, sheep, pigs, cats, and poultry have probably had a multiple origin, and the same is true of many of our varieties of fruits and grains. According to Darwin, our domestic varieties of pigeons, however, are descended from the original blue rock pigeon, *Columba livia*. Through variation and selection there has now arisen an astonishingly large number of varieties, which differ so markedly in structure and appearance that they would unhesitatingly be ranked as distinct species if found in a state of nature.

Man selects the peculiarities of an organism which he wishes to enhance, but Nature, according to the theory of natural selection, is continually preserving those variations which are of service to the organism in the struggle for existence. Natural selection is always working to perfect the adjustment of the organism to its environment. And if man can effect a remarkable amount of modification in the course of a few generations of selective breeding, how great may be the modifications produced by Nature in the course of the ages!

The term "struggle for existence" was used by Darwin "in a large and metaphorical sense." An organism struggles with others of its species when there is a scarcity of food or insufficient space. It may be said to struggle against enemies and parasites, or any competitors which partake of its means of subsistence. It may struggle against adverse conditions of its environment, such as extremes of heat, cold, or drought. The life of every organism is a battle against various forces of the environment that threaten its maintenance. It is a battle in which the losses are high. Many are called, but few are chosen. But the outcome is a stronger and better adapted race of organisms.

The theory of natural selection has come in for a good deal of

rather sentimental criticism because it explains evolution as the outcome of a gruesome process of selective survival. But if the objectors had only paused to reflect that all organisms which have lived have also died, and that just as many animals have died of starvation and just as many lambs have been eaten by wolves whether the fittest survived or not, they would have perceived the futility of their objection. That we live in a world in which organisms are produced with a prodigal hand and are destroyed by the wholesale is simply a fact of observation. Nature is the theater of strife and destruction whether species are the product of a miraculous creation or the survival of the fittest. The selectionists contend that out of the struggle has come the production of higher forms of life, whereas, according to the opposed standpoint, all the cruelty of Nature, which is so much deplored, results merely in a fruitless waste of life.

The theory of natural selection is primarily a theory of how organisms have come to be modified along adaptive lines. The variations with which it works may be in all directions, and from the standpoint of the interest of the individual they may be good, bad, or indifferent. The bad variations are eliminated; the indifferent ones may be tolerated; and the "good" ones tend to be accumulated. Should it greatly profit an insect, for instance, to be colored like its environment, we may suppose that those color variations which most nearly resemble the surrounding colors would be preserved. Through the accumulations of such favorable variations it may be understood how such cases of protective resemblance as the leaf butterfly might finally have been evolved. To quote Mr. Darwin:

> It may metaphorically be said that natural selection is daily and hourly scrutinizing throughout the world, the slightest variations; rejecting those that are bad, preserving and adding up all that are good; silently and insensibly working whenever and wherever opportunity offers at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the lapse of ages, and then, so imperfect is our view into long past geological

ages, that we see only that the forms of life are now different from what they formerly were.

Mr. Darwin believed, as is indicated by the passage just quoted, that the formation of species goes on very slowly through the accumulation of small variations. He was familiar with the fact that extensive variations sometimes occur and that they formed the starting point of a number of domestic varieties of animals and plants, but he believed that such extreme variations, on account of their radical departure from the type, would generally be ill adapted and would tend to die out in a state of nature.

One of the important requirements of a theory of the cause of evolution is that it should explain why organisms tend to become more different from each other in the course of their descent. Theoretically, evolution might occur by all members of a group being modified in a given direction, or it might result in different members being modified along diverging lines. We must of necessity suppose that evolution has pursued the latter course in order to account for the great diversity of species found in nature, and the peculiar grouping into which they fall. The tendency to divergence is brought about, according to Darwin, by the fact that competition is most severe between forms which are most nearly alike. Such forms tend to occupy the same kind of habitats and to subsist upon the same kinds of food. Variations which enable an organism to occupy a somewhat different situation would secure a certain amount of relief from the severity of the struggle for existence. Consequently, Nature puts a premium on diversity. This leads to what Professor Bailey has termed "the survival of the unlike." In the struggle for existence it pays to be different. With a diversity of products Nature can support a greater quantity of life. What we might call the pressure of life forces creatures to adapt themselves to all the situations in which a living being can eke out an existence. And when we consider how Nature has peopled the depths of the sea, the sands of the desert, the caves of the

earth, and the frigid regions of the Arctic Circle, and when we reflect upon the curious shifts for a living which organisms have adopted in order to solve the problem of perpetuating their kind, we cannot fail to be impressed with the severity of the pressure which has forced the organic world into all these diverse habitats and modes of living. It is economic pressure which compels people to follow the diversity of employments in which we find them engaged. Men are not sewer diggers or garbage collectors from choice. Most people get their living as they can and not as they will. Consciously or unconsciously, they are forced into a multitude of activities as a result of competition for a means of subsistence. According to Darwin the formation of species is likewise the consequence of the struggle for existence. Evolution tends not only to go upward or, at times, downward, but it has a strong tendency to go sidewise. Hence the branching and the rebranching of the tree of life.

Darwin's theory of how species came to be formed through natural selection is not without difficulties. One of the most serious of these was pointed out by Mr. Fleeming Jenkin in a very able review of *The Origin of Species*. An incipient variety, according to Jenkin, would not tend to diverge more and more in successive generations; it would be apt to breed with the parental type, and the offspring would tend to do the same. Any differential characters it might possess would sooner or later melt away into the general aggregate, and the new species, therefore, could not get started.

Most of the attempts to meet the objection raised by Jenkin bring into play some form of isolation as a preventive of the swamping effects of intercrossing. Moritz Wagner was one of the first to dwell upon the importance of this factor, and he went so far as to declare that without isolation no species-forming could take place ("Ohne Isolirung keine Arten"). A study of the distribution of closely allied species shows that there is much truth in Wagner's doctrine, especially if we include under isolation other means of preventing intercrossing besides isolation in space. Undoubtedly barriers have a great deal to

do with the formation of distinct species. The several islands of the Galapagos, each with its distinct species of land tortoises, lizards, etc., and the numerous species and varieties of the Achatinellidæ in the several valleys of the Sandwich Islands, are striking illustrations of this fact. If all the Galapagos Islands had been merged into one, and if the Sandwich Islands permitted easy migration of land snails from one valley to the next, it is very doubtful if there would be as many distinct, but closely allied, species on these islands as are now found. Dr. D. S. Jordan remarks:

In regions broken by barriers which isolate groups of individuals we find a great number of related species, though in most cases the same region contains a smaller number of genera and families. In other words, new species will be formed conditioned by isolation, though these same barriers may shut out altogether forms of life which would invade the open district.

Thus, through the eastern United States, unbroken by important barriers, there is but one true species of chipmunk, *Tamias striatus*, and one species of shorelark (*Eremophila alpestris*). In California, broken by many barriers of various sorts, there are a dozen or more different kinds of chipmunks, species and subspecies. But in the eastern states the fauna at large is much greater, because many types of birds and other animals have found entrance there, forms which are excluded from California by the barriers which surround that region.

Dr. Jordan summarizes the facts of distribution of related species by the following statement which has since been designated as Jordan's law:

Given any species in any region, the nearest related species is not likely to be found in the same region, nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort, or at least by a belt of country which gives the effect of a barrier.

We sometimes find closely related species of plants in the same locality, especially if they are self-pollinating. In such cases the species are sexually isolated. Related forms may breed

at different times and thereby become prevented from intercrossing even if they live in the same area. Species of the same genus are often found side by side, but if they are not self-fertilizing they are generally so distinct that they cannot cross, or else they produce progeny which are infertile.

Where closely related groups are not separated by barriers they frequently intergrade where their areas come into contact. Such intergrading groups are generally called subspecies, whereas groups that are clearly distinct, even though closely similar, are ranked as different species. It not infrequently happens that forms from different localities which were at first described as distinct species have been subsequently connected together by intergrading forms discovered in the intervening regions. An instructive instance of this is afforded by the American song sparrow, *Melospiza melodia*. Mr. Ridgway in his *Birds of Middle and North America* describes twenty subspecies of this species, each occupying exclusively a particular range. The typical subspecies is widely distributed over the Atlantic seacoast, the Mississippi valley, and the Great Plains of the western states. Farther west it is replaced by a number of subspecies of smaller areas of distribution. "In California, practically each distinct drainage area has its own peculiar form, one being strictly limited to the salt marshes fringing San Francisco Bay." Other subspecies range southward into Mexico, and northward into Alaska and the Aleutian Islands. Several of these were originally described as distinct species, but they were all merged into one after transitional forms were found in the intervening localities.

The different subspecies of a species generally cluster in a common area, each subspecies being confined exclusively to its own subdivision of the continuous range. In the distribution of the wood rat *Neotoma fuscipes*, one subspecies, *Neotoma fuscipes fuscipes*, occupies an area in California along the coast north of San Francisco Bay. Around the upper end of the Sacramento Valley it intergrades with *N. fuscipes streatori* which ranges southward along the western slope of the Sierras to Kern County, where it intergrades with *N. fuscipes simplex*.

The latter in turn intergrades with *N. fuscipes macrotis* on its western boundary, and *macrotis* is connected by intermediate forms with *N. fuscipes mohavensis* to the north and east.

An analogous grouping of subspecies is repeated hundreds of times over among North American birds and mammals. When Darwin wrote, few connecting links between existing species were known, and much was made of this circumstance by the critics of his theory. But since more attention has been paid to geographical variability numerous intermediate forms have been brought to light. Dr. C. Hart Merriam has stated that "among North American mammals and birds . . . there are more than 1000 species and subspecies, connected with other forms by intergrades." Had Darwin known that connecting links are as common as we now know them to be, one of the chief difficulties that worried him would have been removed.

FIG. 221—Distribution of the subspecies of the wood rat *Neotoma fuscipes*. (After Goldman.)

If we assume that isolation has been an important factor in the formation of species how shall we conceive that it acts? There has been more or less controversy over this question, some writers, among whom is Mr. Gulick, maintaining that isolation *per se* is a cause of divergence independently of natural selection, while others, led by Wallace, contend that isolated forms diverge, because natural selection has adapted them to live in slightly different environments. Whatever the influence of natural selection may be, it is doubtless true that if a

species were separated into different regions the members would become somewhat different as the result of mere isolation. Iso-

FIG. 222—Mutants of beetles of the genus Leptinotarsa: *1*, *L. undecimlineata*; *2*, a mutant (*segregata*) of the preceding; *3-5*, *L. multicincta* (*4*), and its mutants *rubicunda* (*3*), and *melanocarax* (*5*); *6-9*, *L. decemlineata* (*8*), and its mutants *defectopunctata* (*6*), *pallida* (*7*), and *femina* (*9*); *10*, *11*, larvae of *L. multicincta* (*11*), and of *rubicunda* (*10*). (After Tower.)

lated groups, especially if small, tend to become homozygous through inbreeding, and two groups, even with identically the

same inheritance to start with, might happen to become homozygous for different characters.

Most systematists nowadays do not regard all the trifling characteristics which distinguish one species from another as necessarily useful. Many characteristics may arise as small mutations and be preserved because they are not sufficiently injurious to be eliminated by natural selection. It is quite probable that in different isolated groups, different mutations would make their appearance, and this in time might occasion a considerable amount of divergence.

Contrasted with the Darwinian doctrine of the slow formation of species, is the mutation theory which regards species as the product of sudden and stable mutations. The most prominent advocate of this view is the Dutch botanist, Hugo De Vries. Ordinary, or Linnæan, species, according to De Vries, are usually aggregates of smaller subdivisions called elementary species. Elementary species are considered by De Vries to be the product of a single mutation or, more rarely, a very few mutations. In the species *Draba verna*, for instance, more than 200 such forms have been described, a great many of them growing side by side. They are very similar but yet distinct, and the chief reason for their remaining distinct is the fact that they are self-fertilized.

It is with these smaller elementary species that the mutation theory of De Vries is mainly concerned. Originating suddenly, "they are not connected with the parent species by intermediates, and have no period of slow development before they reach the full display of their characters. They do not always arise, but only from time to time. A parent species may produce its offspring separately at intervals, or in larger numbers during distinct mutating periods. After this production, the old species is still the same as it was before, and it subsists in the midst of its children" (De Vries).

It must not be inferred that mutations are necessarily extensive changes; most of them are very small modifications which it takes an experienced eye to detect. Neither should it be in-

ferred that the mutation theory is inconsistent with the doctrine of natural selection. "Some authors," writes De Vries, "have tried to show that the mutation theory is opposed to Darwin's view. But this is erroneous. On the contrary, it is in fullest harmony with the great principle laid down by Darwin." As the same author has elsewhere stated, in referring to natural selection, it "causes the survival of the fittest; but it is not the survival of the fittest individuals, but that of the fittest species by which it guides the development of the animal and vegetable kingdoms."

The differences between the theories of Darwin and De Vries are therefore not fundamental, and, as genetics has advanced, these differences appear to be growing less. Genetic experiments point to the conclusion that mutations depend upon changes in single genes. Such a change might give rise to a new elementary species as defined by De Vries, but there is much evidence that species, as they are commonly distinguished in a state of nature, differ in a great many genes, and hence must have been the product of many mutations. Darwin did not clearly distinguish between germinal and somatic variations; for him a variation was a variation. Modern work in genetics points to the conclusion that somatic modifications have no influence on the production of new forms, and that germinal variations are due to discrete and stable, although it may be very slight, modifications of the germ plasm. Whether the formation of species has taken place mainly by relatively large mutations, such as those which gave rise to the Ancon sheep and the navel orange, or by the accumulation of very small steps, must be determined by a careful analysis of related species as they occur in nature. Theoretically both methods are possible, but, as the experiments of Sumner and of Heustis have shown, even closely related subspecies probably differ in a great many Mendelian factors, and this is indicative of a great many mutations in different genes. Several cases of species crosses have produced a great variety of forms in the F_2 generation, and the knowledge that is slowly accumulating in regard to such crosses indicates

that natural species differ in numerous hereditary factors. Relatively little has yet been ascertained concerning the precise genetic differences of natural species. With fuller knowledge as to what species really are, we shall doubtless come to know more about the steps by which they have come to be formed.

One of the reasons which led Darwin to suppose that species were formed by very gradual stages was the fact that considerable changes may be effected in cultivated plants and domestic animals by the slow process of selection. Species were regarded as plastic material in the hands of the breeder. It is a well established fact that many species can be rather quickly modified by selection, but it is also true that the rate of modification becomes rapidly diminished in successive generations and soon comes to a practical stop. It has been held that the products of this kind of selection are unstable, and tend to revert to the parental type unless selection is kept up. This latter conclusion, however, is not justified, provided that the modified variety is kept from intercrossing. Improved varieties have gone back when selection was discontinued because intercrossing had not been excluded. New types formed by selection are as stable as any others so long as they are kept pure.

But why does selection soon reach a limit? A very probable answer to this question can now be given. It is because many forms consist of mixtures of several hereditary strains, and that selection gradually picks out certain combinations of hereditary factors already in the stock. The longer selection is continued the more nearly the stock becomes homozygous, and when this homozygous condition is attained no further change is produced. At least no further change is produced unless—and this is a very important "unless"—a new mutation happens to arise. We must therefore distinguish between the rapid changes due to the segregation of factors present in a mixed population, and the slower changes produced by the selection of new mutations. Evolution through the selection of occasional mutations can hardly be expected to have occurred at the rapid rate at which man has produced his varieties of dogs, pigeons, and poultry.

It has been objected that there has not been time enough for the process of evolution. We know little as to the rate of evolution, but since the best estimates fix the probable duration of life on the globe at several hundred millions of years, we have no immediate occasion to be disturbed over this objection.

There is, however, strong evidence that the rate of evolution varies enormously in different groups. Many of the one-celled forms of life have persisted with relatively little change ever since the Cambrian period, and the living representatives of the

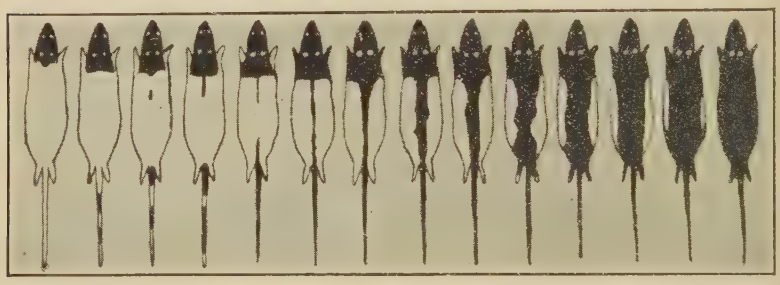

FIG. 223—Grades used to classify the results of selection in hooded rats. From the condition indicated in 0, rats were selected for increased and for decreased area of pigmentation until the differences were produced which are represented by the two ends of the series. (After Castle.)

brachiopod Lingula are no more than specifically distinct from the Lingulas that lived on the old Silurian beaches. Natural selection does not tend to cause all organisms to advance. It is not so much concerned with progressive development as with success in the struggle for existence, and success may be attained by organisms becoming adapted to the various niches they occupy in the economy of nature. Under the proper circumstances adaptation may be best secured through degeneracy from a previously more exalted position in the scale of life. Once embarked upon a career of parasitism, a species may no longer require several of its complex organ systems; in fact, it is better off without them, and therefore natural selection would speed it on the downward path.

There can be no doubt as to the actual operation of natural selection. It has been demonstrated in a number of species that

the death rate is really selective and not purely fortuitous. There can be a question only as to the adequacy of natural selection as an explanation of evolution. On this point we meet with all gradations of opinion among biologists from those who consider that its influence is negligible, to those who are more Darwinian than Mr. Darwin himself. There has been a large amount of discussions as to whether natural selection can account for this or that structure or mode of behavior. It is of course asking much of any theory to require it to explain all the manifold complexities of the organic world. Whether or not the theory is adequate to bear the strain which is placed upon it, no other factor has been proposed which promises to afford a satisfactory substitute.

One consequence of the theory of natural selection is that organisms should not possess, except as a matter of sheer accident, any characteristics which are of exclusive benefit to some other species. From the nature of the case, natural selection can work only for the good of the individual or its kind. The rattle of the rattlesnake could not have been evolved merely to save other animals from being bitten. Its use is primarily for its possessor, and this use is indicated by the historic expression, "Don't tread on me." The so-called warning colorations of animals are supposed to herald the fact that their possessors are *not* good to eat, or are otherwise not safe to meddle with. The conspicuous colors of unpalatable or poisonous animals doubtless saves them from the consequences of a good deal of reckless experimentation on the part of their would-be devourers. Hence warning coloration is supposed to have been evolved on account of its protective value.

The activities of animals are concerned to a large degree with the welfare of other individuals of their kind, and this fact has seemed to many writers to be inconsistent with the theory of natural selection. It should be borne in mind that the individual is not the only unit which functions in the struggle for existence. Natural selection preserves strains, or lines of descent, and it is concerned with individuals mainly in so far as they are the means

of perpetuating the race. If a race of birds were devoid of the proper instincts for taking care of its young it would speedily be eliminated in a contest with another race in which these instincts were normally developed. Proper care for young may, and often does lead to the sacrifice of life on the part of parents. Nevertheless, natural selection may favor the group in which the altruistic instincts are the best developed. In the chapter on "The Evolution of Social Life" it was pointed out that the formation of a society is an adaptive device for enabling animals to solve the problem of perpetuating their kind, and that a society always involves a measure of altruism among its members. Life is not primarily egoistic. The individual organism is always concerned about its successors, even in the simplest forms of life. And as life has evolved, the altruistic activities, which have their root in the perpetuation of the race, come to be more widely extended in the social group, the members of which do not live for themselves alone, any more than organs act for themselves alone in the functioning of the body.

The question of the "all-sufficiency of natural selection" is one of profound philosophic import. The theory attempts to give a naturalistic explanation of the origin of the adaptiveness of the organic world which has long been adduced as evidence of creative design. Darwin spoke of variation as fortuitous, meaning thereby, not that it is purely haphazard, but that it is the outcome of causes whose operation cannot be predicted. Variations occur in many different directions, and natural selection simply accumulates those which happen to be profitable to the organism. According to this theory, the adaptive contrivances of living organisms may be explained as the result of those natural causes which give rise to variability and a differential rate of survival. When we have explained the origin of anything by natural selection, we have made only a preliminary explanation. But no explanations in science are final, as each problem that is solved suggests further problems to be attacked.

Many evolutionists, convinced of the inadequacy of natural

selection to explain the development of organic life, have adopted some form of the doctrine of orthogenesis. Evolution, according to this doctrine, has proceeded along definitely directed lines, and often without regard to utility. Nägeli, who was one of the most prominent advocates of orthogenesis, attributed evolution mainly to an internal "perfecting principle" which works, in obedience to certain definite laws, in causing organisms to become more highly developed. According to the orthogenesis of Eimer, on the other hand, evolution is due chiefly to inherited modifications produced by the environment. Eimer's orthogenesis, therefore, is essentially Lamarckism. The orthogenesists who appeal to internal causes in order to account for evolution have not been very explicit as to just what these internal causes are. Most forms of orthogenesis are statements as to *how* evolution has proceeded rather than *why*. What the causes of evolution may be is still a fertile field for speculation. We shall doubtless need to know much more about the fundamental processes of life than we do at present before the ultimate causes of evolution are revealed.

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CHAPTER XVIII

THE EUGENIC PREDICAMENT

We come now to a consideration of the evolutionary changes occurring in our own species, which is the most important phase of the whole problem of evolution, at least from our point of view. However high man may have risen above the rest of the animal creation, he is still an animal, remarkably similar in structure to his nearest anthropoid relatives, and remarkably like them also in his physiological functions and in his embryonic development. All the facts of human heredity are in harmony with the conclusion that our bodily and mental traits, like those of the lower animals, are transmitted in accordance with Mendel's law, and depend upon the same peculiarities of chromosome behavior. We are part and parcel of the animal creation, and it is fortunate that we are, because, through a study of the lower animals, we learn so very much that is enlightening in regard to ourselves. If all the controverted questions over the causes of evolution discussed in the last chapter were settled, it would be of great assistance to us in grappling with problems of the biological evolution of man. In fact, a very large part of the knowledge that has been gained concerning the life processes of human beings has been obtained by studying other creatures which stand below us in the scale of life.

When we look upon man as the final product of a long period of progressive development, we cannot help being led on to inquire if our present state is the highest which the human race will attain. The doctrine of evolution, which teaches that man has risen instead of fallen, leads us to look forward to the possibilities of further development, and to picture a race of human beings as superior to ourselves as we are superior to Neanderthal man, or his more apelike predecessors. But if we are entitled

to look down upon our poor cousins, the anthropoid apes, a candid contemplation of our physical and mental imperfections and infirmities will force us to admit that there is still a great deal of room for improvement. If one watches the stream of humanity as it files by on the streets of a large city he will readily admit that it would indeed be a pity were the great work of creative evolution to stop with no higher product than the rank and file of present-day humanity.

Francis Galton remarked that "our human civilized stock is far more weakly through congenital imperfection than that of any other species of animals, whether wild or domestic." He was probably right. We have our hereditarily feeble-minded, epileptic, and insane, our hereditarily deaf and blind, our bleeders and albinos; and among the pathological characteristics transmitted by heredity may be mentioned cataract, cleft iris, displaced lens, cleft palate, harelip, atrophy of the optic nerve, progressive muscular atrophy, lack of teeth, abnormal hairiness of body, color-blindness, polydactylism, brachydactylism, fragility of bones, dwarfism, short sight, ichthyosis, chlorosis, cretinism, goiter, diabetes insipidus, and asthma. These are only a few of our hereditary, or partly hereditary ills. Among people whom we consider normal, there are marked hereditary differences in strength, endurance, and vitality. In some families the members are relatively short-lived, seldom living beyond fifty-five or sixty years of age. In other stocks the individuals exhibit an unusual toughness of constitution and frequently live into the nineties. It adds greatly

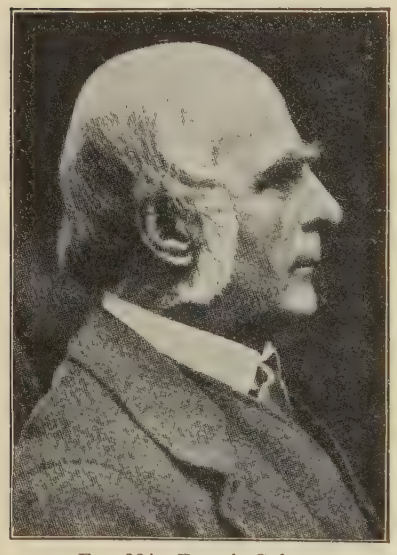

Fig. 224—Francis Galton.

to one's expectation of life to come of long-lived ancestry on both sides.

In respect to its hereditary make-up, humanity is a motley lot. There is probably no other species whose inheritance is so exceedingly diversified. For centuries the inhabitants of different countries have been migrating into other realms and mingling their blood with that of alien peoples. The population of most civilized countries consists of mixtures of mixtures past all possibility of analysis or disentangling.

In a species so highly heterogeneous as our own, there is a

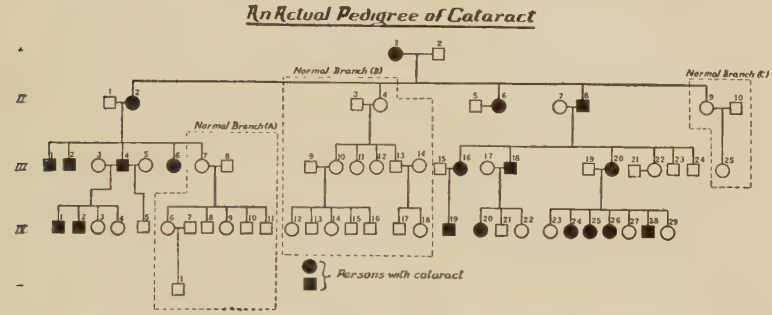

FIG. 225—Pedigree of hereditary cataract. The squares represent males, the circles females. (From Davenport and Laughlin.)

possibility of relatively rapid changes through selective breeding. If one could make the proper selection of parents for a few generations, it would not be difficult to bring about great changes in such characteristics as stature, complexion, color of eyes and hair, shape of head, and the degree of native intelligence. Even the most ardent eugenist does not propose that the mating of human beings should be arbitrarily regulated in the interest of their posterity. But if selective breeding were carried out in the human race, it would be easily possible to effect great changes for better or for worse in a comparatively short time.

When treating of the effects of artificial selection, it was pointed out that the rapid improvements made in many species were mainly brought about by merely taking advantage of the hereditary diversities already existing in the stock. Any change

beyond this has to wait upon the slower appearance of mutations, and these always take their own time about appearing. But disregarding the occurrence of new mutations, and considering only the possible evolution resulting merely from the combination of factors already present in human germ plasm, it is evident that the changes which could be effected in human heredity, would make all the difference between a splendidly endowed human race and a breed of the most wretched degenerates. It lies within the possibilities of human selective breeding to produce either of these extremes, because the race already contains its splendidly endowed stocks, while its breeds of wretched degenerates are only too much in evidence when we inquire into the causes of pauperism, prostitution, and crime.

It is only during the last few decades that we have begun to realize the serious biological and social damage which results from bad heredity. The pedigrees of several degenerate families have been traced for a number of generations, and they have proven to be most instructive in regard to the relation of heredity to the problems of society. One of the most notorious of these is the Juke family, whose history was studied by Mr. Richard Dugdale, and described in his book, *The Jukes*. The family was traced back to a shiftless and intemperate Dutch settler named Max Juke. One of Max Juke's sons married an indolent prostitute known as Ada Juke, who subsequently earned the nickname of "Margaret, the mother of criminals." Of her family of five children, the oldest, who was an illegimate and syphilitic son, married his cousin and produced a family of eight children. Five of the seven daughters were prostitutes, one was idiotic, and the other one enjoyed a good reputation. Ada's first daughter, a prostitute, married a shiftless mulatto and had nine children, of whom the girls became prostitutes, and the men, paupers and vagabonds. Ada Juke's other four sisters produced numerous descendants among whom there was a large number of paupers, prostitutes, and drunkards. Of the 709 Jukes studied by Dugdale, 180 were paupers, or had received poor relief to the extent of 800 years; 60 were habitual thieves; 50 were prostitutes, and

7 were murderers. The cost of this family to the state of New York was estimated at $1,308,000.

Such was the history of the family up to 1875, when Dugdale's study was completed. Through a fortunate circumstance, Dugdale's manuscript, giving the true names of the family (they were called the Jukes because that was not their right name) fell into the hands of the Eugenics Record Office, and Dr. Estabrook undertook to study the further history of this notorious stock. The results of this study were published in a volume entitled *The Jukes in 1915*. The interval between 1875 and 1915 saw a rapid increase in the Juke family with no improvement in its general character. Estabrook's investigations dealt with 2094 individuals, of whom 1258 were living when the report was made. Up to date, there had been 299 paupers or pensioners on public charity; 118 were criminals; 378 were prostitutes; 86 kept brothels; and the record of the family for intemperance, illegitimacy, and general worthlessness was of the same kind that was described by Mr. Dugdale.

One of the significant facts brought out by Estabrook's investigation was that the Jukes were characterized by a high percentage of mental defect. According to Estabrook, "One-half of the Jukes were, and are, feeble-minded, mentally incapable of responding normally to the expectations of society, brought up under faulty environmental conditions which they consider normal, satisfied with the fulfillment of natural passions and desires, and with no ambition or ideals in life." All of the criminals of this family whom Estabrook had an opportunity to study were feeble-minded. "Willett, who committed murder; VI 529, a low-grade imbecile who committed burglary; Edgar, a rapist; and VI 16, who committed assault, are all mental defectives, and in none of these has their criminal record biased the writer in diagnosing their mentality."

Another family, now equally notorious, is the Kallikak family, whose history has been described by Goddard. The investigation of this family began with the effort to trace the ancestry of a feeble-minded girl, Deborah, who was confined in a home for

the feeble-minded in Vineland, New Jersey. Deborah's mother was feeble-minded and had borne several other children by various men. The study of Deborah's more remote ancestry led back to a Martin Kallikak, a soldier in the Revolutionary War. Martin had a son by a feeble-minded girl, but later he married into a respectable family and produced several children whose descendants became eminently respectable and noteworthy members of the community. The son of the feeble-

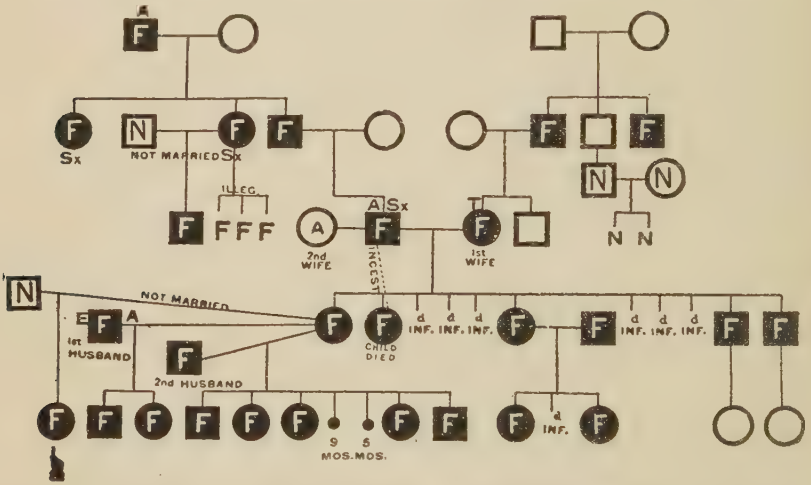

FIG. 226—Heredity of feeble-mindedness. The squares represent males, the circles females. The dark squares and circles indicate feeble-mindedness. *A*, alcolohic; *E*, epileptic; *N*, normal; *d. inf.*, died in infancy. Note that when both parents are feeble-minded all the children who grow up are feeble-minded also. (After Goddard.)

minded girl, named, with probably unintentional irony, Martin Kallikak, Jr., was later known as the "Old Horror." Martin, Jr., had a family of ten children, most of whom were a bad lot. The oldest, Millard, the direct ancestor of Deborah, married a feeble-minded woman belonging to a feeble-minded family and produced fifteen children. Nearly all of these children who grew up were known to be feeble-minded. One of them, the grandfather of Deborah, was mentally defective, and married a dull woman of feeble-minded stock. There were eleven children, most of whom were feeble-minded and produced feeble-minded

progeny. Among the 480 descendants of the original feeble-minded girl, 36 were illegitimate; 33 were sexually immoral, mostly prostitutes; 24 were confirmed alcoholics; 8 kept houses of ill-fame; 3 were criminals, and 3 were epileptics. According to Goddard, 143 "were or are feeble-minded, while only forty-six have been found normal. The rest are unknown or doubtful."

Similar family histories have been traced with the Tribe of Ishmael, the Hill Folk, the Nam Family, the Zero family, the Pineys, the dwellers in the Vale of Siddem, and several others, but these illustrations must suffice. The study of such families as these is especially illuminating in relation to the causes of crime, delinquency, and vice. Crime is not hereditary as such, but persons may be predisposed to crime by virtue of hereditary defects of intellect or emotional balance. Lombroso's doctrine that the "born criminal" is set apart from the rest of humanity by certain anthropological characters has been shown to be open to serious objections. Much evidence points to the conclusion that the hereditary basis of crime is largely feeble-mindedness, although a tendency to epilepsy and other forms of abnormality is also found to an unusual degree in the criminal population. The outcome of several investigations of the mentality of the inmates of prisons and reformatories shows that about one-fourth of the population of these institutions are feeble-minded and that a considerable proportion of the remainder fall into the group ranging from dull normal to average intelligence. There are, of course, a few persons of superior mentality who become imprisoned for their misdeeds. Such persons are relatively infrequent in the prison population, partly because they are more successful in evading justice, and partly because they are more able to see the probable consequences of criminal acts. The more intelligent are also, as a rule, in a better economic status, and are not under the same temptation to commit crimes against property. The habitual criminal, or recidivist, the man who is convicted again and again for infractions of the law, is usually a person with some inborn defect or abnormality of mind.

Studies of the mentality of prostitutes, vagrants, paupers, and juvenile delinquents, reveal much the same percentage of mental defects that occurs among criminals. It is the stocks such as the Jukes and Kallikaks that form the great recruiting ground for our large army of offenders. They constitute a great burden which is not measured merely by the hundreds of millions which they cost the state. The damage which is wrought as a result of the vice, the venereal disease, and the bad moral influence disseminated by these stocks among the better elements of the community, is a far greater cost than the money which is directly expended on their account.

A good deal of the shortcomings of these families has been attributed to the bad influence of their environment. If the Jukes and Kallikaks had all been raised under ideal conditions, doubtless they would not have turned out nearly so badly. But it should be borne in mind that the bad environment under which these people are reared is itself largely the product of their bad heredity. Low mentality and feeble inhibitions (the two generally go together) will in the long run be productive of ignorance, poor economic status, and a tradition of moral laxity and vice. The more intelligent elements of society tend in course of time to rise out of a condition of ignorance and squalor, but the mentally defective remain on the same low level and constitute the kind of poor who are always with us. The bad environment which a defective stock tends to create operates to prevent individuals from rising out of it. *It is a fact of the greatest importance that, sooner or later, bad heredity makes bad environment, and that good heredity makes good environment.* Could we start all kinds of people with the same advantages of education, it would probably not be many generations before the Jukes, the Kallikaks, and the Tribe of Ishmael would be living under much the same surroundings in which we find them today.

There is an old saying, "It takes all kinds of people to make a world." It is true that all kinds of people are required to make the world as it is, but it is also true that the world would be much better off if many of its kinds of people were not here.

Inferior breeds of human beings are among the greatest handicaps of our civilization. The culture and the intellectual advance of the race are the product of its best minds. Take away the most intelligent ten per cent of its population, and any

FIG. 227—Three microcephalic brothers. Mental tests showed that none of these boys gave a mental age of more than four years. There were two other microcephalic defectives in the same family and five other siblings who were normal. (After Dr. C. Bernstein.)

nation would sink to a relatively low level of intellectual productivity. Under such conditions, Greece would never have seen the Age of Pericles, nor would civilization have made its

rapid advances in the nations of modern Europe. There is no measure of the debt of humanity to Plato, Aristotle, Shakespeare, Goethe, or Pasteur. The best blood of a nation is its most priceless possession. To be composed of people endowed with a superior heredity of mind and body is perhaps the greatest blessing that can fall to the lot of any country. On the other hand, one of the greatest misfortunes that could afflict a country would be to be composed of such degenerate breeds of humanity as we have just described. The great bulk of the population of all countries lies between these two extremes, but it can be readily modified in the direction of either one. Which way is our own population actually going?

The answer to this question depends upon what kinds of people are producing the largest numbers of children who live to maturity. But this again depends upon two factors: the birth rate, and the death rate. In order to ascertain if the race is improving or deteriorating, we should have to be able to compare the birth rates and the death rates of the members of superior and of inferior stocks. There have been several investigations of this problem and their general results are in practical agreement in pointing to the conclusion that the better endowed stocks tend to be replaced by those of inferior heredity. Let us consider some of the evidence for this conclusion.

Most civilized countries have witnessed a decline of the birth rate during the last fifty or seventy-five years.[1] In France the decline set in still earlier and it has proceeded to such an extent that the population has been nearly stationary for several years. The birth rate began to fall in Great Britain and Germany about 1876, somewhat later in Austria and Italy, and still later in Russia and the Balkan states. Nevertheless, nearly all

[1] One very important aspect of the birth rate is its relation to overpopulation and the expansion of peoples. When a people is faced with the alternatives of starvation or expansion it will generally take the latter course. This frequently entails war with neighboring peoples. The pressure of population has been a chronic incentive to conflict throughout the course of human history. It has doubtless furnished the real cause of war in numerous cases in which various other reasons have been assigned.

countries in Europe increased greatly in population during the nineteenth century, partly as the result of their great industrial development, and partly on account of the reduction of the death rate which was brought about by the advances made in medicine and hygiene. The decline in the birth rate is not the result of either fewer or later marriages, since it has occurred in countries in which the marriage rate has not declined nor the average age at marriage increased. A large part of it is due to the voluntary limitation of the size of the family. This being true, it is not surprising that the greatest decline should have occurred among the more intelligent, educated, and thrifty members of the community. The several studies which have been made of the families of graduates of colleges have shown that the college-bred population does not produce enough children to rescue it from extinction. With our present death rate and marriage rate it requires three or more children per family to keep a stock from decreasing in numbers. The average number of children for the graduates of Harvard from 1860 to 1890 was a little over two per married graduate, and, for all graduates, considerably less than two. The record for Yale and several other colleges is much the same. With the graduates of women's colleges the record is still lower. Only a little over fifty per cent of women graduates marry at all, and those who marry produce, on the average, less than three children per family. Our college-bred men and women are coming to constitute a larger and larger percentage of the population, and in mentality, they certainly stand somewhat above the general average of humanity. High-school graduates have larger families than the graduates of colleges, but they have smaller families than those who have had no more than a common-school education. The professional classes—lawyers, doctors, etc.—have very small families, and the same is true of successful men of affairs. Cattell has found that the average size of the completed family among American men of science is 1.88 children.

The decline of the birth rate which began in the more culti-

vated strata of society has been extending gradually to other classes. Among the skilled artisans and the more thrifty and enterprising workers in general, the practice of family limitation has been steadily growing. The custom of restricting the birth supply has had the least effect upon the more ignorant and improvident, who go on reproducing their kind without restraint in the primitive animal fashion. Among those who attempt to avoid the responsibilities and burdens of more children, recourse is only too frequently had to abortion. Since it involves the destruction of an embryo which is developing into a human being, abortion, unless necessary to safeguard the life of the mother, is adjudged a crime in most civilized countries. Nevertheless, there is much evidence that the traffic in this form of child murder is a flourishing business, and that it is the cause of much damage to the health of women who take this way of escaping from the responsibilities of maternity. Miss Elderton, who has made a valuable study of the causes of the decline of the birth rate in the north of England, finds that abortions and other means of restricting the family are coming to be widely practiced among the more thrifty workers. On the other hand, "the poorest classes of all, those who cannot provide for themselves, but seek public dispensaries and maternity charities for attendance, do not appear to limit their families, for very many have large families running up to thirteen or more."

A study by Professor Karl Pearson and his colleagues of the relation between size of family and the quality of the parents, brought out the fact that a large number of children was correlated with low rent, dirty houses, poor food, low wages of the father, and irregularity of employment. If we should explain the low rent and poor food as in part the result of family size, there would seem to be no reason why a large family should cause wages to be low, or employment to be irregular. Wages are at least a rough measure of the intelligence and efficiency of the worker, and the fact that low wages and large families go together is doubtless because both result from the ignorance and improvidence of the fathers.

When we come to the positively feeble-minded, we find that fecundity is usually quite unrestrained. Whetham remarks:

Feeble-minded women, whether married or unmarried, are remarkably fertile. The workhouse records frequently note that five, six, or seven children have been born before the mother is twenty-five years of age, and she herself may have commenced childbearing at fifteen years of age or even younger. Most of these children inherit the mental condition of their parents, and where both parents are known to be feeble-minded, there is no record of their having given birth to a normal child. In one workhouse there were sixteen feeble-minded women who had produced between them 116 children with a large proportion of mental defect. Out of one such family of fourteen, only four could be trained to do remunerative work.

With regard to the fertility of feeble-minded stocks, it has been pointed out that the feeble-minded children from the degenerate families, who use the special schools in London, come, sometimes two or more at a time, from households averaging about seven offspring, whereas the average number of children in the families who now use the public elementary schools is about four.

Dr. Wilmarth, in speaking of the transmission of mental defect, has incidentally furnished an illustration of the high fertility of feeble-minded stocks:

Two children from one family are under our care. From the sheriff, who brought the children, and an intelligent neighbor, I learned that the mother was weak mentally. The father seldom worked but managed to raise his family on what he could obtain in other ways. Not one of the eighteen children was a desirable member of society. The girls drifted into disreputable lives; the boys were idlers and thieves with no moral sense. I know a couple in Pittsburgh, Pennsylvania, whose nine children were all idiots of low grade. A family in eastern Wisconsin, the father and mother are both feeble-minded; at least seven of the eight children are imbeciles; five we have cared for. A couple in this state have nine children, all subnormal, and there are several, to my knowledge, in collateral branches of the family. One feeble-minded woman, now removed from the state, had by different men eighteen children in nineteen years, she alleges. I have seen

only three of her children. These were feeble-minded and especially defective in moral sense.

Citations like the foregoing might be multiplied a hundredfold, but they are perhaps sufficient to illustrate the preponderating fecundity of subnormal humanity. It is true that the poorly endowed are afflicted by a relatively high death rate. Infant mortality in degenerate stocks is especially high. The children, perhaps, are as vigorous as any, but they suffer from the ignorance and folly of their parents, and from the bad environment in which they are reared. But, notwithstanding their high infant mortality, the ravages of venereal disease, and the other unwholesome accompaniments of ignorance and squalor, stocks like the Jukes and Kallikaks somehow flourish like the green bay tree. Perhaps other degenerate strains may have become extinct as the result of their excesses or misfortunes, but there can be no doubt about the extinction of the classes which have made their mark by virtue of their intellectual achievements. Among the people who are not reproducing themselves we must include the graduates of our colleges and universities, the more successful men of business, and an increasingly large number of intelligent and capable women who are choosing an independent career instead of the old-fashioned occupations of domestic life. Seventy-five years ago such stocks, according to the studies of Heron, were contributing their quota to the population, but at present the race is losing its best inheritance. The drain is increasing in magnitude as time goes on. Education is being extended to a wider and wider circle of those whose native ability permits them to acquire it. Our ideal has been to open the doors of opportunity as widely as possible so as to permit every one to advance in proportion to his natural talents. The attainment of this ideal would doubtless be very desirable from the standpoint of present social welfare; but so long as success is correlated with race suicide, it would only intensify the present tendencies that are working toward racial decadence.

Our civilization has brought about a very anomalous relation between success and fertility. In the animal world the individuals which are the most successful usually produce the largest number of offspring, but in our present social life, the types who attain the dominant positions are generally marked for extinction. Those who should have the most children commonly have the fewest, while those who should have few children, or none at all, usually have the most. From the eugenic standpoint this is obviously a very unfortunate situation. Unquestionably, the balance should somehow be restored. So far as the feeble-minded and other hereditarily defective classes are concerned, the procedure of either sterilization or segregation under conditions which would prevent propagation, should doubtless be adopted. To a certain extent, both of these methods are already employed, but they do not succeed in eliminating more than a small fraction of our degenerates. It seems entirely feasible to restrict the propagation of defectives much more completely than is now done, and if this were carried out thoroughly for a few generations, it would doubtless go far toward reducing our burdens of crime and delinquency.

The most important problem, however, is not so much the elimination of our worst heredity as the increase of our best stocks. This is also the most difficult problem. It is much easier to decree that the defectives shall produce less children than it is to induce superior people to produce more. Whatever methods are successful in achieving this latter end must be based upon a widespread appreciation of the eugenic situation. The ignorance which prevails in regard to matters of racial obligation, is appalling. One finds educated women remarking glibly that "two children are quite enough," and justifying the limitation of the family to one or two children by such phrases as "Quality is better than quantity," quite unmindful of the fact that, in a very few generations of such restriction, there would be neither quality nor quantity. Of course, women should not exhaust themselves by excessive childbearing, but each family whose qualities are worth perpetuating should have, on the

average, at least the mimimum number of children required to insure its continuation. This is a matter of elementary moral obligation which should be obvious to every one. Nevertheless, it is not appreciated, I fear, by a large proportion of educated people.

With a wider diffusion of knowledge of heredity and the elementary principles of eugenics, it is perhaps not too much to hope that more people who are hereditarily well endowed will pay heed to this obligation. Knowledge of heredity and eugenics will be racially valuable also on account of its influence on marriage selection; and it will be especially valuable in affording a rational basis for public sentiment in favor of measures for racial improvement. Every nation which is solicitous for the sound heredity of its people should see to it that those whom it admits as immigrants are of good stock and likely to produce children who will enhance, rather than deteriorate the eugenic quality of its inhabitants. If civilized nations ever succeed in checking the drain of their best blood, which is now going on to an ever increasing extent, this can be accomplished only on the basis of a general knowledge of the principles of eugenics, and a willingness to put such knowledge into practice. Whether society will rescue itself from its present eugenic predicament is uncertain. Its fate is in its own hands. We are in one respect better situated than the peoples of older civilizations which have crumbled into decay—we have some knowledge of the biological factors which are responsible for racial improvement and racial deterioration. We can diagnose our racial ills. And we should, if we are wise enough, be able to supply the remedy.

There is little likelihood that our civilized humanity will remain long in its present unstable biological status. Changes of composition are inevitable. Deterioration is easy, and may be difficult to avoid. But our race has great possibilities of further development if it can only conquer the forces which are insidiously working to undermine its inheritance.

"It may be that the gulfs will wash us down;
It may be we shall touch the Happy Isles."

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GLOSSARY

NOTE TO THE STUDENT IN REGARD TO TECHNICAL TERMS

In the following glossary, which is added for the convenience of the student, I have given the derivation as well as the definition of many of the technical terms which are used in the text. A large part of our college population in these days is totally ignorant of Latin, and a larger part has never become acquainted with Greek. But even those who are not classical students may profit by cultivating the habit of looking up the etymology of words. One may easily acquire a stock of root words which give the clue to the meaning of a large number of technical terms. The common Greek and Latin prefixes and suffixes can be mastered in a very short time. Every college student is presumably going to be occupied with intellectual pursuits, to a greater or less extent, during the rest of his life, and he should therefore attempt to gain some insight into the make-up of the words he frequently encounters. He should at least learn the Greek alphabet in order to make the best use of an English dictionary.

Aboral (Lat. *ab*, from; *os*, mouth), opposite the mouth.

Afferent (Lat. *ad*, to; *ferre*, to carry), a term applied to nerves carrying impulses toward a center.

Albumin (Lat. *albumen*, white of egg), a protein occurring in the white of eggs.

Alveoli (Lat. *alveolus*, a small cavity), small cavities or spaces resembling cells.

Amino acid, an acid containing the amino group NH_2.

Amitotic (Gr. *α*, without; *μίτος*, thread), without mitosis, a term applied to cell division.

Amœboid (Gr. *ἀμοιβή*, change), like an Amœba.

Amphibia (Gr. *ἀμφι*, both; *βίος*, life), a class of vertebrates including frogs, newts, and related forms.

Anabolism (Gr. *ἀναβολή*, that which is thrown up), constructive metabolism.

Anaërobic (Gr. *ἀν*, not; *ἀήρ*, air; *βίος*, life), capable of living without free oxygen.

Antheridium (Gr. *ἀνθηρός*, flower), an organ producing male sex cells in ferns and other flowerless plants.

Anthropoid (Gr. *ἀνθρωπος*, man), manlike. Applied to the higher apes.

Antitoxin (Gr. *ἀντί*, against; *τοξικόν*, poison), a substance which neutralizes a poison.

Arachnida (Gr. *ἀράχνη*, spider), a group of arthropods including spiders, scorpions, mites, etc.

Archegonium (Gr. *ἀρχή*, beginning; *γόνος*, fruit), an organ bearing female sex cells in ferns and other flowerless plants.

Artery (Gr. *ἀρτερία*, artery), a vessel carrying blood from the heart.

Arthropod (*ἄρθρον*, joint; *πούς*, foot), a phylum of invertebrate animals with segmented bodies and jointed appendages.

Aster (Gr. *ἀστήρ*, star), a starlike body appearing during mitotic cell division.

Atavism (Lat. *atavus*, ancestor), a reversion to an ancestral type.

Bast, the phloëm part of fibrovascular tissue.

Biology (Gr. *βίος*, life; *λόγος*, discourse), the science of life.

Blastopore (Gr. *βλαστός*, germ; *πόρος*, passage), the mouth of the gastrula.

Blastula (diminutive of *βλαστός*, germ), an embryonic stage consisting of a hollow sphere of cells.

Brachiopods (Gr. *βραχίων*, arm; *πούς*, foot), a group of invertebrates with bivalved shells resembling those of bivalved molluscs, but belonging to a very different group.

Calyx (Gr. *κάλυξ*, a cup), the outer whorl of floral organs.

Cambium (Lat. *cambio*, exchange), the growing layer between wood and bark.

Cambrian, the first division of the Paleozoic era; named from Wales (Lat. *Cambria*).

Carboniferous (Lat. *carbo*, coal; *ferre*, to bear), a prominent coal-bearing period of the Paleozoic era.

Carnivora (Lat. *caro*, flesh; *vorare*, devour), a flesh-eating order of mammals, including cats, wolves, and their allies.

Castration (Lat. *castrare*, to castrate), the removal of the sex organs.
Catalysis (Gr. *κατάλυσις*, dissolution), the acceleration of a chemical transformation by a substance which is not destroyed in the process.
Cellulose, the carbohydrate forming the cell wall of plants.
Centrosome (Gr. *κέντρον*, center; *σῶμα*, body), a small body occurring at the poles of the spindle in mitotic cell division.
Cephalopoda (Gr. *κεφαλή*, head; *πούς*, foot), a group of molluscs including the squid, octopus, nautilus, and many extinct relatives.
Cercaria (Gr. *κέρκος*, tail), the tailed larva of a fluke.
Cestode (Gr. *κεστός*, a girdle), a tapeworm.
Chlorophyll (Gr. *χλωρός*, green; *φύλλον*, leaf), the green coloring matter of plants.
Chordata (Gr. *χορδή*, cord), a phylum of animals having a notochord.
Chromatin (Gr. *χρῶμα*, color), a deeply staining substance of the nucleus.
Chromosomes (Gr. *χρῶμα*, color; *σῶμα*, body), a (usually) thread-like body of chromatin appearing in mitotic cell division.
Cilia (Lat. *cilium*, eyelash), hairlike processes of cells.
Cœlenterate (Gr. *κοῖλον*, cavity; *ἔντερον*, gut), a member of a phylum of invertebrates including hydroids, jellyfish, corals, etc.
Cœlom (Gr. *κοῖλον*, cavity), the space between the intestine and body wall in the Cœlomata.
Colloids (Gr. *κόλλα*, glue), substances with aggregated molecules which do not ordinarily diffuse through membranes.
Corolla (Lat., little wreath), the usually colored whorl of floral organs next above the calyx.
Cranium (Gr. *κρανίον*, skull), the brain case.
Cretaceous (Lat. *creta*, chalk), a subdivision of the Mesozoic era represented in some localities by chalky deposits.
Crustacea (Lat. *crusta*, crust), a group of arthropods including crabs, crayfish, shrimps, and their allies.
Cyst (Gr. *κύστη*, sac), a protective envelope surrounding an organism in a resting stage.
Cytology (Gr. *κύτος*, cell), the study of cells.
Cytoplasm (Gr. *κύτος*, cell; *πλάσμα*, formative material), the protoplasm of a cell outside the nucleus.

Dendrite (Gr. *δένδρον*, tree), a branching process of a nerve cell.
Devonian, a period of the Paleozoic named from Devonshire.

Dextrose (Lat. *dexter*, right), a sugar commonly found in fruits.

Diatom (Gr. δίς, double; ἄτομος, indivisible), a unicellular plant with a bivalved siliceous shell.

Dimorphism (Gr. δίς, double; μορφή, form), having two forms.

Dorsal (Lat. *dorsum*, back), pertaining to the back.

Echinoderm (Gr. ἐχῖνος, hedgehog; δέρμα, skin), a phylum of invertebrates including starfishes, sea urchins, crinoids, and their allies.

Ectoderm (Gr. ἐκτός, outside; δέρμα, skin), the outer germ layer of the embryo.

Ectoplasm (Gr. ἐκτός, outside; πλάσμα, formative material), the outer part of the protoplasm of cells.

Edentates (Lat. *ex*, out; *dens*, tooth), an order of mammals including the sloth, armadillo, anteater, and more numerous extinct species.

Efferent (Lat. *ex*, out; *ferre*, to carry), a term applied to nerves which carry impulses away from a center.

Endocrine (Gr. ἔνδον, within; κρίνω, I separate), pertaining to organs of internal secretion.

Endoderm (Gr. ἔνδον, within; δέρμα, skin), the inner germ layer of the embryo.

Endomixis (Gr. ἔνδον, within; μῖξις, mingling), nuclear reorganization without conjugation.

Endoplasm (Gr. ἔνδον, within; πλάσμα, formative material), the inner part of the protoplasm of cells.

Enzyme (Gr. ἐν, in; ζύμη, a ferment), a ferment.

Eocene (ἠώς, dawn; καινός, recent), the earliest period of the Tertiary.

Epidermis (Gr. ἐπί, upon; δέρμα, skin), the outer layer of the skin.

Epigenesis (Gr. ἐπί, upon; γένεσις, origin), the doctrine that development proceeds from a simple, unorganized germinal substance.

Eugenics (Gr. εὖ, good; γένεσις, origin), a study of the agencies that affect the quality of the human breed.

Eustachian tube (Eustachius, an Italian anatomist), the passage from the middle ear to the pharynx.

Fauna (Lat. *Faunus*, god of shepherds), the animal life of a region.

Femur (Lat. *femur*, thigh), the thigh bone.

Fission (Lat. *fissio*, cleavage), the division of a cell or organism into two or more parts.

Flagellum (Lat. *flagellum*, a little whip), a lashlike process of a cell.
Flora (Lat. *flos*, flower), the plant life of a region.
Frond (Lat. *frons*, leaf), a leaflike expansion of one of the lower plants.

Gamete (Gr. γαμέτης, spouse), a sex cell.
Gametophyte (Gr. γαμέτης, spouse; φυτόν, plant), a plant bearing sex cells; the sexual generation.
Ganglion (Gr. γάγγλιον, swelling), a group of nerve cells.
Gastrula (Gr. γαστήρ, belly), the two-layered stage of the embryo.
Gene (Gr. γένεσις, origin), a hereditary factor.
Genetics (Gr. γένεσις, origin), the science dealing with heredity and variation.
Germ layer, one of the fundamental layers of the embryo; ectoderm, entoderm, mesoderm.
Gland (Lat. *glans*, nut), an organ of secretion.
Glycogen (Gr. γλυκύς, sweet; γένεσις, origin), a form of carbohydrate (animal starch) found in the liver and other parts.
Gonad (Gr. γόνος, reproduction), an organ producing sex cells.

Hæmoglobin (Gr. αἷμα, blood; Lat., *globus*, globe), the red oxygen-carrying protein of the red corpuscles.
Hepatic (Gr. ἧπαρ, liver), relating to the liver.
Hermaphrodite (Gr. Ἑρμῆς, Hermes; Ἀφροδίτη, Aphrodite), an organism with both sexes combined.
Heterozygous (ἕτερος, different; ζυγωτός, joined), an organism with different genes for a given character.
Histology (Gr. ἱστος, web; λόγος, discourse), the science of tissues.
Holophytic (Gr. ὅλον, altogether; φυτόν, plant), typically plantlike in nutrition.
Holozoic (Gr. ὅλον, altogether; ζῷον, animal), animal-like in nutrition.
Homology (Gr. ὁμολογία, agreement), structural similarity due to descent.
Homozygous (Gr. ὅμος, like; ζυγωτός, linked), having like factors for a given character.
Hormone (Gr. ὅρμων, that which sets in motion) an internal secretion.

Intussusception (Lat. *intus*, within; *suscipere*, to take up), the addition of material throughout the mass.
Invertebrate (Lat. *in*, not; *vertebra*, backbone), an animal without a backbone.

Jurassic, a subdivision of the Mesozoic era represented in the Jura Mountains.

Karyokinesis (Gr. *κάρυον*, nut; *κίνησις*, motion), mitotic or indirect cell division.

Katabolism (Gr. *καταβολή*, throwing down), destructive metabolism.

Larva (Lat. *larva*, mask), an immature but active stage of an animal differing markedly from the adult.

Leucocyte (Gr. λευκός, white; *κύτος*, cell), a white corpuscle of the blood.

Linin (Gr. λίνον, thread), the protoplasmic framework of the nucleus.

Lipoid (Gr. λίπος, fat), a substance allied to the fats.

Lymph (Lat. *lympha*, clear water), a clear fluid containing white corpuscles and occurring in the lymph vessels, or lymphatics.

Macronucleus (Gr. *μακρός*, large; Lat. *nucleus*, kernel), a large nucleus, contrasted with the micronucleus.

Malaria (Italian, *mal' aria*, bad air), a disease characterized by chills and fever caused by a species of Plasmodium.

Mammalia (Lat. *mamma*, breast), a class of vertebrates which suckle their young.

Marsupial (Lat. *marsupium*, pouch), an order of mammals which carry the young in a pouch.

Medusa (Gr. Μέδουσα, a Gorgon), a jellyfish.

Meganucleus (Gr. *μέγας*, large, Lat. *nucleus*, kernel), a large nucleus. Same as macronucleus.

Mesoderm (Gr. *μέσος*, middle; *δέρμα*, skin), the middle germ layer, between ectoderm and endoderm.

Mesoglœa (Gr. *μέσος*, middle; *γλοιά*, glue), a noncellular layer in Cœlenterates between entoderm and ectoderm.

Mesozoic (Gr. *μέσος*, middle; *ζωή*, life), the middle geological era between the Paleozoic and the Cainozoic, or Tertiary.

Metabolism (Gr. *μεταβολή*, change), the chemical transformations occurring in living substance.

Micronucleus (Gr. *μικρός*, small; Lat. *nucleus*, kernel), a small nucleus, a term used when there is a larger nucleus in the same organism as in the Infusoria.

Miocene (Gr. *μείων*, less; *καινός*, recent), a subdivision of the Tertiary era.

Mitosis (Gr. *μίτος*, thread), indirect cell division, so called because threadlike structures make their appearance.

Monotreme (Gr. *μόνος*, one; *τρῆμα*, opening), a member of the most primitive order of mammals, including the duckbill and spiny anteater.

Morphology (Gr. *μορφή*, form; *λόγος*, discourse), the science of structure.

Mutation (Lat. *mutatio*, change), a discrete, stable germinal variation.

Nautilus (Gr. *ναυτίλος*, sailor), a cephalopod mollusc with chambered shell.

Nectary (Gr. *νέκταρ*, drink of the gods), the part of a flower that secretes honey.

Neuron (Gr. *νεύρον*, nerve), a nerve cell with its branches.

Notochord (Gr. *νῶτον*, back; *χορδή*, cord), a chord of cells forming the beginning of the backbone in vertebrate animals.

Nucleolus (Lat. diminutive of *nucleus*, kernel), a small, rounded body found in the nucleus.

Oligocene (Gr. *ὀλιγος*, few; *καινός*, recent), a period between the Eocene and the Miocene in the Tertiary.

Ontogeny (Gr. *ὄν*, being; *γεν*, birth), the development of the individual.

Ordovician, a subdivision of the Paleozoic era.

Osmosis (Gr. *ὠσμός*, pushing), diffusion through semi-permeable membranes.

Ovary (Lat. *ovum*, an egg), the organ producing eggs.

Ovule (Lat. *ovulum*, diminutive of *ovum*), the beginning seed of a flowering plant.

Ovum (Lat. *ovum*, an egg), an egg.

Paleontology (Gr. *παλαιός*, old; *ὄν*, being; *λόγος*, discourse), the science of extinct forms of life.

Paleozoic (Gr. *παλαιός*, old; *ζωή*, life), the earliest era in which fossils are abundant although life occurred throughout long preceding periods.

Pancreas (Gr. *πάν*, all; *κρέας*, flesh), a large gland opening into the intestine and secreting the pancreatic juice.

Parenchyma (Gr. *πάρεγχυμα*, filling material), soft cellular tissue which is relatively undifferentiated.

Parthenogenesis (Gr. *παρθένος*, virgin; *γένεσις*, origin), the development of eggs without fertilization.

Pentadactyl (Gr. *πέντε*, five; *δάκτυλος*, digit), having five digits.

Peristalsis (Gr. *περιστέλλω*, I constrict), a wavelike constriction passing along a muscular tube.

Permian (from Perm in Russia), the last period of the Paleozoic era.

Petrifaction (Lat. *petra*, rock; *factus*, made), an organism converted into stone.

Phagocyte (Gr. *φαγεῖν*, to eat; *κύτος*, cell), a leucocyte that engulfs foreign materials.

Phloëm (Gr. *φλοιός*, bark), the outer part of a fibro-vascular bundle: it forms bark in exogenous plants.

Photosynthesis (Gr. *φῶς*, light; *σύνθησις*, putting together), the formation of carbohydrates by green plants under the influence of light.

Phylogeny (Gr. *φῦλον*, branch; *γένεσις*, origin), the ancestral development of a group.

Placenta (Lat. a flat cake), an organ of attachment, a term applied to the attachment of seeds to the ovary in plants, and of embryos to the uterus in animals.

Plasma (Gr. *πλάσμα*, formative material), the fluid part of the blood or lymph.

Plastid (Gr. *πλαστής*, one who forms), protein bodies in cells which are concerned in forming certain products.

Pleistocene (Gr. *πλεῖστος*, most; *καινός*, recent), the last period of the Cainozoic era.

Pliocene (Gr. *πλείων*, more; *καινός*, recent), a late period of the Tertiary era.

Polydactylism (Gr. *πολύς*, many; *δάκτυλος*, digit), having supernumerary fingers or toes.

Preformation, the theory that the parts of the embryo are preformed in the germ.

Primates (Lat. *primus*, first), the order of mammals including the monkeys, apes, and man.

Prothallus (Lat. *pro*, in place of; *thallus*, young branch), the sexual generation of ferns and other flowerless plants.

Protista (Gr. *πρῶτος*, first), a group including the primitive one-celled organisms, both plant and animal.

Protophyta (Gr. *πρῶτος*, first; *φυτόν*, plant), the one-celled plants.

Protoplasm (Gr. *πρῶτος*, first; *πλάσμα*, formative material), living matter.

Protozoa (Gr. *πρῶτος*, first; *ζῷον*, animal), one-celled animals.

Pseudopodia (Gr. *ψευδής*, false; *πούς*, foot), a protoplasmic projection such as occurs in an amœboid organism.

Pulmonary (Lat. *pulmo*, lung), pertaining to the lungs.

Pylorus (Gr. *πυλωρός*, gate-keeper), the constriction between the stomach and small intestine.

Recapitulation theory, the doctrine that individual development is an epitome of the development of the race.

Receptor (Lat. *receptor*, receiver), a sense organ.

Recessive (Lat. *recessus*, receding), not appearing in the presence of the dominant character.

Regression (Lat. *regressus*, going back), a return toward the mean of the group.

Renal (Lat. *rena*, kidney), pertaining to the kidneys.

Secretion (Lat. *secretus*, separated), the separation of a substance by living tissue, as when the liver secretes bile.

Segregation (Lat. *segregare*, to separate out), separating out.

Sepals (Lat. *sepes*, enclosure), the parts of the calyx.

Serum (Lat. *serum*, whey), the fluid of the blood after removal of the clot.

Silurian (Lat. *Silures*, an ancient tribe of Wales), a period of the Paleozoic era

Somatic (Gr. *σῶμα*, body), relating to the body.

Spermatocyte (Gr. *σπέρμα*, sperm; *κύτος*, cell), a cell that gives rise to spermatids that develop into spermatozoa.

Spermatozoa (Gr. *σπέρμα*, sperm; *ζῷον*, animal), mature male germ cells.

Sporophyte (Gr. *σπορά*, seed; *φυτόν*, plant), a plant which bears spores; the asexual generation.

Symbiosis (Gr. *σύν*, together; *βίος*, life), the mutually beneficial association of two species.

Synapsis (Gr. *σύναψις*, conjunction), a pairing of chromosomes previous to reduction.

Tertiary (Lat. *tertius*, third), a geological era between the Mesozoic and the Quaternary.

Thyroid (Gr. *θυρέος*, a shield), an endocrine gland near the larynx.

Triassic (Gr. *τριάς*, three), the earliest period of the Mesozoic, so named from its three subdivisions.

Trilobite (Gr. *τρεῖς*, three; *λοβός*, lobe), a primitive extinct crustacean.

Trypsin (Gr. *τρύειν*, to wear down), a ferment of the pancreas which digests proteins.

Urea (Gr. *οὖρον*, urine), a nitrogenous compound $(NH_2)_2CO$ formed by the decomposition of proteins.

Uterus (Lat. *uterus*, womb), a modified part of the oviduct in which embryos are carried.

Vacuole (Lat. *vacuus*, empty), a space in a cell usually filled by some product of protoplasmic activity.

Vascular (Lat. *vasculum*, a little vessel), pertaining to vessels of some kind.

Vein (Lat. *vena*, vein), a vessel carrying blood toward the heart.

Ventricle (Lat. *ventriculus*, a little belly, or venter), a cavity, especially a chamber of the heart that forces blood into an artery.

Vertebrate (Lat. *vertebra*, a joint), an animal having a backbone, or vertebral column.

Vitamine (Lat. *vita*, life; *amin*, a chemical radicle), an accessory food substance very important in maintaining life.

Viviparous (Lat. *vivus*, alive; *parere*, to bear), bringing forth living young.

Xylem (Gr. *ξύλον*, wood), the woody part of a fibrovascular bundle.

Zoölogy (Gr. *ζῷον*, animal; *λόγος* discourse), the science of animals.

Zygote (Gr. *ζυγωτός*, joined together), a product of the fusion of two cells in sexual reproduction.

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